Seasonal changes in nutritional condition of shorebirds (charadrii) during the non-breeding seasons

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SEASONAL CHANGES IN NUTRITIONAL CONDITION OF SHOREBIRDS (CHARADRII) DURING THE NON-BREEDING SEASONS

by

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To my wife, Sue

and daughter, Katherine.

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ABSTRACT

The nutritional condition (fat and protein reserves) of shorebirds was studied, mainly at Teesmouth and Lindisfarne, north-east England, during the non-breeding season.

Normal patterns of fat and protein storage are similar in most coastal shorebird species. Fat reserves rise to a peak in midwinter. Fat is stored rapidly before both spring and autumn migrations. Protein reserves (measured as pectoral muscle size) remain steady during winter. Protein reserves increase before spring migration, but not before autumn migration. Most shorebirds regulate both fat and protein reserves during winter. Plovers (Charadriidae) have larger fat and protein reserves than Sandpipers (Scolopacidae). However rocky-shore species carry smaller reserves than species feeding on soft sediments. Interspecific differences are related to morphology, foraging behaviour, habitat use and winter movements. First-year shorebirds carried similar sized or larger reserves than adult conspecifics.

Catabolism of nutritional reserves was studied during two periods of severe winter weather in north-east England. Reserves were catabolised faster by species that normally carried the largest regulated reserves. In eastern Britain some Redshanks cannot regulate their fat and protein reserves even during mild winters. Possible reasons are discussed. The condition of shorebirds that had starved to death during severe weather is examined. Redshanks, first-year Oystercatchers, inland species, and shorebirds that return early to breeding grounds are most at risk. Recovery of nutritional condition after starvation is examined.

In addition to seasonal variation, differences in the size of regulated fat reserves occur in different wintering grounds. Total lean weights in relation to wing-length as a measure of body size are used to examine whether similar seasonal and latitudinal differences in protein reserves of shorebirds exist. Plovers have larger pectoral muscles than Sandpipers but similar total lean weight (measured in relation to body size). During winter, lean weights are lower in several equatorial and southern hemisphere areas than in northern temperate regions. Seasonal and latitutinal changes in lean weight are discussed in relation to periods of environmental stress.

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GENERAL INTRODUCTION

All birds need nutritional reserves for use when they are unable to find food fast enough to satisfy their energetic and metabolic demands.

Fat is the main energy reserve stored by most birds (Blem 1976). More than twice the energy is released during catabolism of fat (9.1 kcal. g^{-1}, Johnston 1970) than of muscle protein or carbohydrate (Hazelwood 1972). In spite of this, the main energy reserve of the Willow Grouse, Lagopus lagopus, (Grammeltvedt 1978) and Spruce Grouse, Dendragapus canadensis, (Pendergast & Boag 1973), is muscle protein. In other species this is normally used as an energy source only after fat reserves have been exhausted (Davidson 1981, Papers 1 and 2). Protein stored in skeletal muscle is primarily used as a source of replacement amino acids for protein synthesis (Millward 1970, Kendall, Ward & Bacchus 1973, Evans & Smith 1975, Jones 1980).

Many shorebirds (Charadrii) that breed in arctic, subarctic and northern temperate regions spend their non-breeding season on northern temperate coasts. On these sites, shorebirds frequently encounter severe weather conditions, particularly low temperatures and high winds. The birds may then suffer temporary periods of negative energy balance both because of increased energetic requirements (e.g. Dugan et al. 1981) and decreases in rates of food intake (e.g. Goss-Custard et al. 1977a, Evans 1976, 1979, Pienkowski 1980a). Shorebirds overwintering in these areas need fat and protein reserves for survival through periods of negative nutritional balance (Evans & Smith 1975).

On northern temperate coasts, many studies of winter feeding ecology and behaviour have now been made on shorebirds. These include the following species: Redshank, Tringa totanus, (e.g. Goss-Custard 1966, 1969, 1970a, 1976, 1977a), Oystercatcher, Haematopus ostralegus, (Drinnan 1958, Norton-Griffiths 1967, Heppleston 1971, Hulscher 1976), Bar-tailed Godwit, Limosa lapponica, (Smith & Evans 1973, Smith 1975), Knot, Calidris canutus, (Prater 1972, Dugan 1981a), Ringed Plover, Charadrius hiaticula, (Pienkowski 1980a, b), Grey Plover, Pluvialis squatarola (Pienkowski 1980a, b, Dugan 1981a, Townshend 1981a), Curlew, Numenius arquata (Townshend 1981a, b), Sanderling, Calidris alba (Myers, Connors & Pitelka 1979, Myers 1980, Brearey 1981) and Turnstone, Arenaria interpres (Harris 1979, Brearey 1981). Several studies have also been made on groups of species on single estuaries such as the Wash (Goss-Custard 1977b, Goss-Custard et al. 1977a, b), Teesmouth (Pienkowski 1973, Evans et al. 1979, Evans 1980b), Lindisfarne (Pienkowski 1980b) and the Dutch Waddensee (Smit & Wolff 1981, Zwarts in press).

Despite this extensive knowledge of feeding adaptations in wintering shorebirds, there are few published studies of nutritional condition as an adaptation to winter survival of shorebirds in northern temperate regions. The only relevant account of seasonal changes in nutritional condition is by Evans & Smith (1975) for Bar-tailed Godwits at Lindisfarne, N.E. England. Fragmentary information on the fat reserves of Dunlins on the Wash (Pienkowski, Lloyd & Minton 1979), Redshanks and Knots on Morecambe Bay (Prater 1975) and Redshanks on the Ythan, N.E. Scotland (Goss-Custard 1966) is also available. Other studies of the fat reserves of shore-

birds during winter refer to equatorial or southern hemisphere areas, e.g. Venezuela (McNeil 1970), South Africa (Elliott et al. 1976, Summers & Waltner 1979), New Zealand (Baker 1975), Tasmania (Thomas & Dartnall 1970) and Wake Island, Pacific Ocean (Johnston & McFarlane 1967), where adverse environmental conditions seldom occur and there is little storage of nutritional reserves. In the northern hemisphere, most work on shorebird nutritional condition has concerned fat deposition during autumn and spring migration periods, in both the Americas (Johnston 1964, McNeil 1969, McNeil & Cadieux 1972a, Page & Middleton 1972, Rundle 1980) and Europe (Mascher 1966, Mascher & Marcstrom 1976). Most studies have examined only fat reserves. Few, except Evans & Smith (1975), have also investigated protein reserves, although these have been documented in other orders of birds, including geese (Hanson 1962, Ankney 1977), grouse (Pendergast & Boag 1973) and passerines (e.g. Baggott 1975, Jones & Ward 1976, Fry, Ferguson-Lees & Dowsett 1972, Fogden & Fogden 1979).

This thesis is presented as three papers, the first a comparative study of the nutritional condition, as measured by fat and protein reserves, of nine species of shorebirds during the non-breeding seasons in north-east England where they face some of the most severe winter weather conditions anywhere in the British Isles (Dugan 1981a) and so might be expected to try to store large fat and protein reserves. The information presented in the first paper outlines the normal pattern of fat and protein reserves in each species, i.e. those reserves maintained in the absence of environmental stress. It concentrates on winter levels of condition, but condition in

autumn and spring is also discussed. The use of nutritional reserves during severe weather is discussed in Paper 2, and seasonal and latitudinal differences in lean weights of shorebirds are presented in Paper 3.

Appendices 1 and 2 present additional information relevant to Papers 1 and 2. Appendix 1 concerns loss of weight and condition during short-term captivity, and Appendix 2 presents formulae for the estimation of lean weight and fat from live shorebirds.

Publications quoted in this general introduction are listed in the references to Paper 1.

Paper 1. The nutritional condition of shorebirds (Charadrii) in north-east England during the non-breeding seasons

INTRODUCTION

Seasonal cycles of weight and nutritional condition occur widely in vertebrates, including mammals (e.g. Evans 1973, Sinclair 1974, 1975) and birds (e.g. Hanson 1962, Ward 1969, Evans 1969a, b, Evans & Smith 1975, Blem 1976, Jones & Ward 1976), and also in invertebrates (e.g. Hancock & Franklin 1972, Chambers & Milne 1975, Dugan 1981a). These cycles are usually associated with the storage and use of fat and protein reserves before and during migration, breeding and food shortage. Seasonal weight cycles in wintering populations of shorebirds have been documented from many northern temperate intertidal areas including the Wash (Branson 1979), the Waddensee (Smit & Wolff 1981), Morecambe Bay (Prater 1975, Dare 1977, Clapham 1978) and the Ythan estuary (Goss-Custard 1966, Heppleston 1971). Changes in the total body weight of shorebirds involve changes both in fat reserves (Goss-Custard 1966, Evans & Smith 1975, Prater 1975) and protein reserves (Evans & Smith 1975). Details of these are available for rather few species in northern temperate areas.

The questions addressed in this paper are threefold. Firstly, in what ways are seasonal cycles of fat and protein reserves adaptive; secondly, why do differences in condition between birds of different ages arise; and thirdly, how do interspecific differences in condition relate to differences

in feeding, habitat use and migration? There has been no previous comparative study of the nutritional condition of shorebirds using one northern temperate wintering area.

Extensive studies of shorebird biology at Teesmouth (Pienkowski 1973, Evans et al. 1979, Davidson 1980, Goodyer & Evans 1980, Dugan 1981a, b, Townshend 1981a, b, Brearey 1981) and Lindisfarne (Smith & Evans 1973, Smith 1975, Millard 1976, Pienkowski 1981b) provide information on the ecology, behaviour and movements of most species of shorebirds examined in this study, in the areas from which specimens were obtained.

METHODS

Collection of Shorebirds

The nutritional condition of 400 individuals of nine species of shorebirds was examined (Table 1). Specimens were collected at two intertidal areas in north-east England, Teesmouth and Lindisfarne (Figure 1). These sites are the only important intertidal sand and mudflats on the east coast of Britain between the Humber estuary (170 km. south of Teesmouth) and the Inner Firth of Forth (150 km. north-west of Lindisfarne). The coastal distance between Teesmouth and Lindisfarne is 130 km.(80 miles).

Samples of shorebirds were collected during most non-breeding seasons between 1971/72 and 1978/79 for various purposes, using several collection methods (Table 2). Between 1971/72 and 1974/75 various shorebirds were shot under licence from the Nature Conservancy Council (NCC) for gut content analyses (Smith 1975, Millard 1976, Evans et al. 1979). Nutritional condition in Bar-tailed Godwits collected during

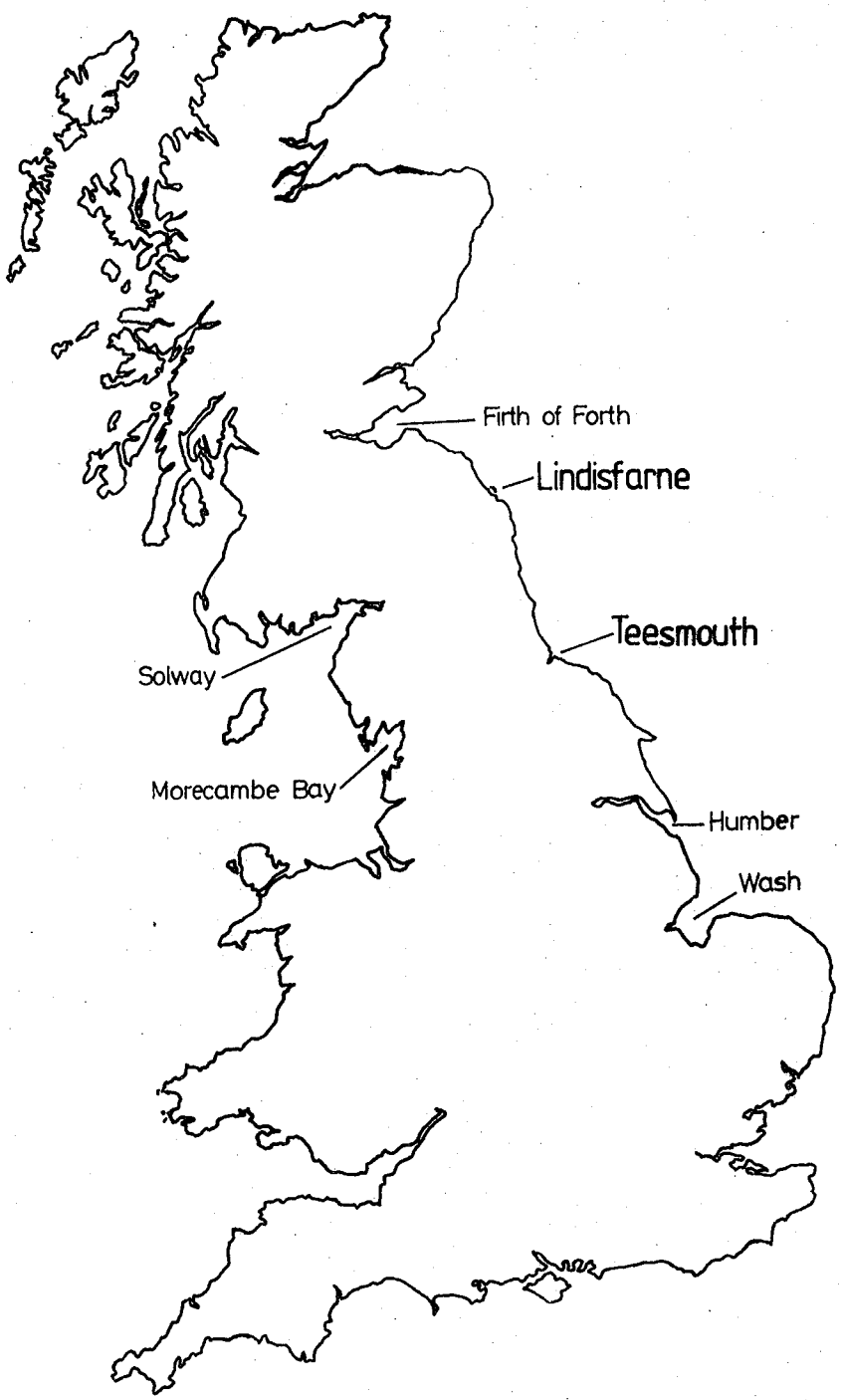

Figure 1: Location of Teesmouth and Lindisfarne, and adjacent estuaries.

Table 1. Numbers of shorebirds from Teesmouth and Lindisfarne analysed for nutritional condition.

	Adult	First -year	Total
Ringed Plover, *Charadrius hiaticula*	8	0	8
Golden Plover, *Pluvialis apricaria*[a]	22	1	23
Grey Plover, *Pluvialis squatarola*	3	0	3
Knot, *Calidris canutus*	57	20	77
Sanderling, *C. alba*	15	4	19
Dunlin, *C. alpina*	118	99	217
Bar-tailed Godwit *Limosa lapponica*[b]	21	14	35
Curlew, *Numenius arquata*[c]	13	0	13
Turnstone, *Arenaria interpres*	4	1	5

[a] Golden Plovers cannot be reliably aged in winter (Prater, Marchant & Vuorinen, 1977). All birds collected after October were treated as adults.

[b] These birds supplement the collection of 170 examined by Evans & Smith (1975).

[c] Age of Curlews unknown: all treated as adults.

Table 2. Locations, methods and reasons for collection of shorebirds analysed for nutritional condition.

Species	Year(s)	Area[a]	Collection method[b]	Reason for collection[c]
Ringed Plover	1976-79	T	C	3
Golden Plover	1972	L	S	1
	1978	L	S	4
Grey Plover	1973	L	S	1
	1978	T	C	3
Knot	1972-73	T	S	1
	1977-78	T	C	2,3
Sanderling	1972-73	T	S	1
	1977-79	T	C	3
Dunlin	1971-73	L,T	S	1
	1975-79	T	C,M	3
	1977-78	T	C	2
Bar-tailed Godwit	1977-78	L	S	4
Curlew	1971-74	L,T	S	1
Turnstone	1975-76	T	C	3

[a] L = Lindisfarne, T = Teesmouth

[b] S = shot, C = cannon-net, M = mist-net

[c] 1 = gut content analysis, 2 = heavy metal analysis
3 = netting casualty, 4 = body condition during severe weather

these years has been examined by Evans and Smith (1975). Their data have been re-analyzed where appropriate. The nutritional condition of Redshanks collected in 1971/72 and 1972/73 is examined in Paper 2. In 1977 and 1978, Bar-tailed Godwits and Golden Plovers were shot at Lindisfarne under licence from the NCC for this study, to examine any changes in nutritional condition induced by severe weather (Paper 2).

Other samples were collected as a result of netting at Teesmouth. During May 1977 and September 1977 - May 1978 Dunlins and Knots were collected at monthly intervals under licence from the NCC at Teesmouth for analysis of heavy metals by the Institute of Terrestrial Ecology (Evans & Ward in prep.). These samples were randomly selected from catches made using cannon-nets. All other specimens analysed were incidental casualties from netting activities; mainly from cannon-netting with a few Dunlins also from mist-netting.

Any variations in nutritional condition due to diurnal or tidal feeding cycles were minimised since all samples were caught at about the same state of tide, High Water minus 2 hours - High Water, at roosts, and samples were shot as they moved from feeding grounds to high tide roosts.

Several problems in the collection of specimens resulted in many samples being small, and collected irregularly. ~~In~~ When ~~shot samples~~ shooting, large samples could not often be obtained due to difficulties in approaching birds closely (Millard 1976). For netted samples the major problem was in making large catches on a regular basis, mainly because of unpredictable variations in the use of roost sites at Teesmouth. The lack of data for most species in March and April results from

difficulties in catching the small populations present at that time of year (see Figures 21 and 23).

Cannon-net catches sample variable proportions of the shorebird population. There is evidence from marked shorebirds that individuals are non-randomly distributed within roosting flocks at Teesmouth and elsewhere (Pienkowski & Dick 1976, Furness & Galbraith 1980, L.R. Goodyer pers. comm.), so most catches are probably of population sub-groups. In some samples this has been associated with detectable changes in nutritional condition: these are discussed later.

Differences might exist in the nutritional condition of shot and netted samples, but any biases in shot samples are also unknown. No differences in nutritional condition attributable to method of collection were detected.

Laboratory Analysis of Nutritional Condition

Birds were weighed on Pesola balances, whenever possible, immediately after death, to give a total body weight (TBW). Carcasses were then deep-frozen until required for analysis. While carcasses were thawing, each was aged on plumage characteristics, and wing-length and bill-length measured. Shrinkage in these measurements was negligible whilst deep-frozen. Methods of condition analysis were those used by Evans and Smith (1975) so the results from this study are directly comparable with their analyses of Bar-tailed Godwits.

After a carcass had thawed, the pectoral muscles (pectoralis, supracoracoideus and coracobrachialis) from the right side were removed after any subcutaneous fat had been cleared from their surface. The abdomen was opened and the liver and kidneys removed for separate analysis, in preparation

for heavy metal studies. Carcasses were sexed by examination of the gonads.

The pectoral muscle, liver, kidneys and remaining carcass were separately dried to constant weight in vacuum ovens at 50°C. In Dunlins, and so probably in other species, drying at 50°C resulted in a slightly, but not significantly, lower loss in weight (mean water content 67.5% of total lean weight) than the 68.6% in Dunlins dried at 80°C but not in vacuo (Pienkowski et al. 1979). An oven temperature of 50°C ensures that little, if any, fat is lost during the drying process. Loss of fat can otherwise be substantial, particularly in very fat specimens (Johnston & McFarlane 1967).

After drying, samples were weighed, giving dry weight (DW), and fat was extracted in a Soxhlet apparatus using 60° - 80°C b.pt. petroleum ether as solvent. Fat from pectoral muscle, liver and kidney was extracted for a minimum of six hours, from the residual carcasses of small species for a minimum of 12 hours, and from those of large species by repeated washing in petroleum ether for a minimum of three days. Samples were then redried to constant weight: the lean dry weight (LDW). Weight of fat was calculated as DW minus LDW, and the total weight of fat found by adding weight of fat from the separately analysed components. Total lean weight (LW) was calculated as total body weight minus fat.

About 1% of the fat extracted using these techniques probably consists of structural rather than labile reserve lipids, since in studies of several species (Ward 1969, Newton 1969, Fogden & Fogden 1979, Marcstrom & Mascher 1979, Davidson unpubl.) residual levels of 1 - 1.5% lipids were

found even in birds that had died of starvation. This residual level is consistent between species and any shorebird carrying less than 2% fat has little or no labile fat reserve.

Calculation of Condition Indices

Calculations and definitions are summarised in Table 3 and follow Evans & Smith's (1975) terminology. Fat levels are examined as a lipid index: weight of fat as a percentage of total body weight. This lipid index is not directly related to potential survival time because this is a function of metabolic rate which in turn varies with body weight to the power of approximately 0.75 (Evans and Smith 1975, Kendeigh, Dol'nik & Gavrilov 1977). Large species thus require slightly lower lipid indices than small species if they are to survive on their fat reserves for the same time. These differences are outweighed by the effects of other factors on lipid levels (see later). Interspecifically, since females are larger than males in most shorebirds, they might be expected to carry lower lipid incides than males, but no significant sex differences have been detected during the non-breeding season in this or other studies (Johnston & McFarlane 1967, Evans & Smith 1975, Mascher & Marcstrom 1976, Pienkowski et al. 1979).

Pectoral muscle size is used as a measure of protein reserves (Kendall, Ward & Bacchus 1973, Evans & Smith 1975). Two indices have been calculated:

1) Lean dry pectoral muscle as a proportion of a standard muscle volume (V), calculated from four measurements of the skeletal attachment of the pectoral muscle (Figure 2).

Table 3. Definitions and calculations of nutritional condition measurements

Lipid Index % (LI)	$LI = \frac{\text{Fat (g.)}}{\text{total body wt. (TBW)(g.)}} \times 100$
Pectoral Muscle Index (SMV)	a) $V = b(ad + 0.433c^2)$ (see Fig.2) b) $\text{Index} = \frac{\text{Lean dry pect. muscle (g.)}}{V}$
Pectoral Muscle Index (% LW)	$\text{Index} = \frac{\text{Lean dry pect. muscle (g.)}}{\text{Total lean wt. (LW) (g.)}} \times 200$
Water Content (%)	$\text{Water Content} = \frac{\text{Water (g.)}}{\text{Lean Wt. (g.)}} \times 100$
Liver Index (%)	$\text{Liver Index} = \frac{\text{Lean dry liver (g.)}}{\text{Total lean dry wt. (g.)}} \times 100$
Liver Lipid Index (%)	$\text{Liver Lipid Index} = \frac{\text{Liver fat (g.)}}{\text{Dry liver (g.)}} \times 100$
Lean Weight (g.)	LW = total body wt. (g.) - Fat (g.)
Lean Dry Weight (g.)	LDW = LW - Water (g.)

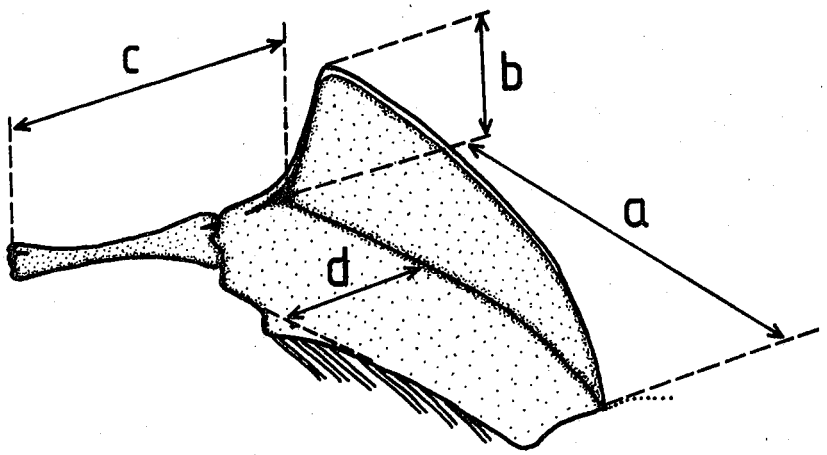

Figure 2: Skeletal measurements (cm.) of the sternum and coracoid bone used to calculate the area of attachment of the pectoral muscles and the standard muscle volume, V (see Table 3).

The standard muscle volume, for one pectoral muscle, is calculated as

$$V = b\,(ad + 0.433c^2)$$

where 'a' to 'd' are measured in centimetres. The Pectoral Muscle Index (SMV) is calculated from lean dry pectoral muscle as a proportion of V.

2) The weight of both lean dry pectoral muscles as a percentage of total lean weight, abbreviated as Pectoral Muscle Index (% LW). This index measures the relative changes in pectoral muscles and total lean weight: if both change to the same extent, this index will not change.

Changes in total lean weight (LW) per se cannot be readily examined because a) as most shorebirds are sexually dimorphic, lean weight variability is great, necessitating subdivision of samples into sex- and age-classes, and resulting in reduced sample sizes, and b) even within a single age- and sex-class, size and weight variation is up to 15% of the mean (Evans and Smith 1975). Therefore lean weights are examined only in some species. Seasonal trends in shorebird lean weights in north-east England and elsewhere are discussed further in Paper 3. Total lean dry weight (LDW) is also examined in some species, as is water content (weight of water as a percentage of total lean weight) which remains constant when water changes in constant proportion to changes in lean dry weight.

Liver condition is an indicator of metabolic state rather than nutritional condition (Farner 1960, King, Barker and Farner 1963, Evans and Smith 1975), and is examined only where

it aids interpretation of seasonal changes in fat and protein levels.

Corrections for Missing Data

Many of the specimens originally collected for gut content analysis were missing some internal organs when nutritional condition came to be analysed. Corrections to the total weight of fat, lean weight and lean dry weight were made using mean weights of the missing organs for the relevant age, sex and season in each species. Total body weights were also unavailable for some of these specimens, and were estimated from the addition of the mean percentage water content for the relevant species and season, and the weight of fat, to total lean dry weight.

Dunlins and Knots collected in May 1977 and September 1977 - May 1978 (for heavy metal analyses) under licence from the NCC had to be kept for between 4 and 24 hours between capture at Teesmouth and being killed in the laboratory at Durham, because parts of the carcass required to be frozen in liquid nitrogen immediately after death (for enzyme studies) and liquid nitrogen could not be taken to Teesmouth. During their period of captivity these birds catabolised some fat and protein and so their nutritional condition is not directly comparable with that of birds killed immediately on capture. Their loss of condition during captivity is documented in Appendix 1, and the rates of weight loss derived there have been used to extrapolate back to the nutritional condition of these birds at capture.

Estimation of Nutritional Condition in Live Birds

The lean weights of some shorebirds were used to derive formulae for the estimation of fat in live birds from measures

of body size (Appendix 2). It was intended to apply these techniques to total body weights of live birds measured during netting at Teesmouth, to produce a more complete seasonal pattern for some species. However, the technique has proved (so far) of more limited application than hoped, mainly due to limitations arising from small sample sizes of weights collected on each catch date in previous years. The technique allows estimation only of lipid levels, a major assumption being the stability of lean weight during a season. A recently-developed technique for estimation of pectoral muscle size (Davidson 1979a) may allow examination of seasonal changes in the pectoral muscle size of live birds, but insufficient measurements are available as yet. For some species whose fat reserves could not be estimated, seasonal changes in total body weight of live birds are examined where they contribute to an understanding of nutritional reserves.

Statistical Analysis of Results

Data were analysed using both parametric and non-parametric statistics, using methods from Bailey (1959) and Sokal & Rohlf (1969). Additionally, some analyses were performed on computer, using programs in the SPSS package (Nie et al. 1975). Percentages were corrected using angular transformations (Sokal and Rohlf 1969) before comparison in statistical tests.

RESULTS

The results of analyses of seasonal changes in nutritional condition are presented below for each shorebird species. Emphasis is placed on fat levels (lipid indices) and pectoral muscle size (as an indicator of protein reserves). Total body weights, total lean weights and water contents are detailed only where appropriate.

During the non-breeding season, variations in the weight of fat (Table 4) accounted for between 46% (adult Knots) and 87% (adult Grey Plovers) of the variations in total body weight encountered in this study. Similar relationships have been reported for Pacific Golden Plovers, Pluvialis dominica fulva on Wake Island, Pacific Ocean (Johnston & McFarlane 1967), for first-year Dunlins in southern Sweden (Mascher & Marcstrom 1976) and for Semipalmated Sandpipers, Calidris pusilla in Ontario (Page & Middleton 1972). In most shorebirds the slope of the regression of total weight on fat is greater than unity (Table 4). This increased slope may be partly caused by variations in body size since most shorebirds in this study exhibited reversed sexual dimorphism (i.e. females are larger than males). However the relationship still holds even when data from the two sexes are analysed separately (see Dunlin, Table 4), indicating that an increase in total body weight involves other components in addition to fat. Simultaneous increases in both fat and protein reserves, particularly during spring (see later) lead to slopes of greater than unity. Slopes of less than unity (Ringed Plovers and Grey Plovers) were probably a result of small sample sizes.

Table 4. Correlations between the weight of fat (g.) and total body weight (g.) in shorebirds during the non-breeding season in north-east England.

Species		n	r	r^2	slope	intercept	P
Dunlin	Ad. male	35	.924	.854	1.42	44.90	<.001
	Ad. female	42	.853	.728	1.24	49.07	<.001
	1st yr. male	23	.920	.846	1.37	42.41	<.001
	1st yr. female	37	.896	.803	1.61	45.81	<.001
Knot	Ad.	29	.681	.464	2.22	102.95	<.001
	1st yr.	19	.748	.560	1.06	110.64	<.001
Bar-tailed Godwit	Ad.	23	.729	.531	2.62	240.25	<.001
	1st yr.	15	.723	.523	2.15	237.79	<.002
Sanderling	Ad. + 1st yr.	12	.888	.789	1.12	48.16	<.001
Turnstone	1st yr.	5	.893	.797	1.53	82.94	<.050
Ringed Plover	Ad.	8	.763	.582	0.77	62.92	<.050
Grey Plover	Ad.	5	.933	.870	0.87	214.77	<.050
Golden Plover	Ad.	22	.892	.796	1.36	160.38	<.001

Ringed Plover, Charadrius hiaticula L.

Eight adult Ringed Plovers from Teesmouth were analysed for nutritional condition. Their lipid indices are shown in Table 5. Of three birds from late August, one carried 29% fat and, like some Grey Plovers in September (Figure 4), was probably preparing for further migration, and two others had lipid indices averaging 6%. One Ringed Plover had the very high lipid index of over 30% in late November. Other Ringed Plovers included two birds from late April with an average of 9.7% fat. They may have begun to increase their fat levels in preparation for migration. By late May, two migrant Ringed plovers were carrying substantial fat reserves (lipid indices of 17.5% and 26.5%). Total body weights of Ringed Plovers reached a midwinter peak on Morecambe Bay in December (Figure 3). Weights of the few catches of Ringed Plovers from Teesmouth also show evidence of a midwinter peak (Figure 3). Assuming a mean lean weight of 63 g. in winter (calculated from Appendix 2), Ringed Plovers in late November had an estimated lipid index of 25%. In Ringed Plovers, pectoral muscle size as a proportion of SMV (Table 6) was consistently above 0.3. The single bird in November had very large pectoral muscles (0.37 SMV). Pectoral muscles of Ringed Plovers in late May were slightly higher than in late April. In August, the bird carrying a large fat load had slightly larger pectoral muscles (0.313 SMV) than those with less fat (0.306, 0.297 SMV). Pectoral muscles as a percentage of total lean weight varied from 6.0% in August to 7.8% in November (Table 6).

Table 5. Lipid indices of Ringed Plovers at Teesmouth

Date	n	Lipid index (%)
25.08.77	1	28.80
	2	6.25 ± 0.6
23.11.76	1	30.40
24.04.78	2	9.70 ± 0.2
25.05.79	2	22.00 ± 4.4

Values are mean ± 1 standard error.

Table 6. Pectoral muscle size of Ringed Plovers at Teesmouth

Date	n	Pectoral muscle index	
		SMV	% LW
25.08.77	3	.305 ± .004	6.04 ± 0.11
23.11.76	1	.370	7.78
24.04.78	2	.319 ± .010	6.69 ± 0.39
25.05.79	2	.325 ± .016	6.72 ± 1.06

Values are mean ± 1 standard error

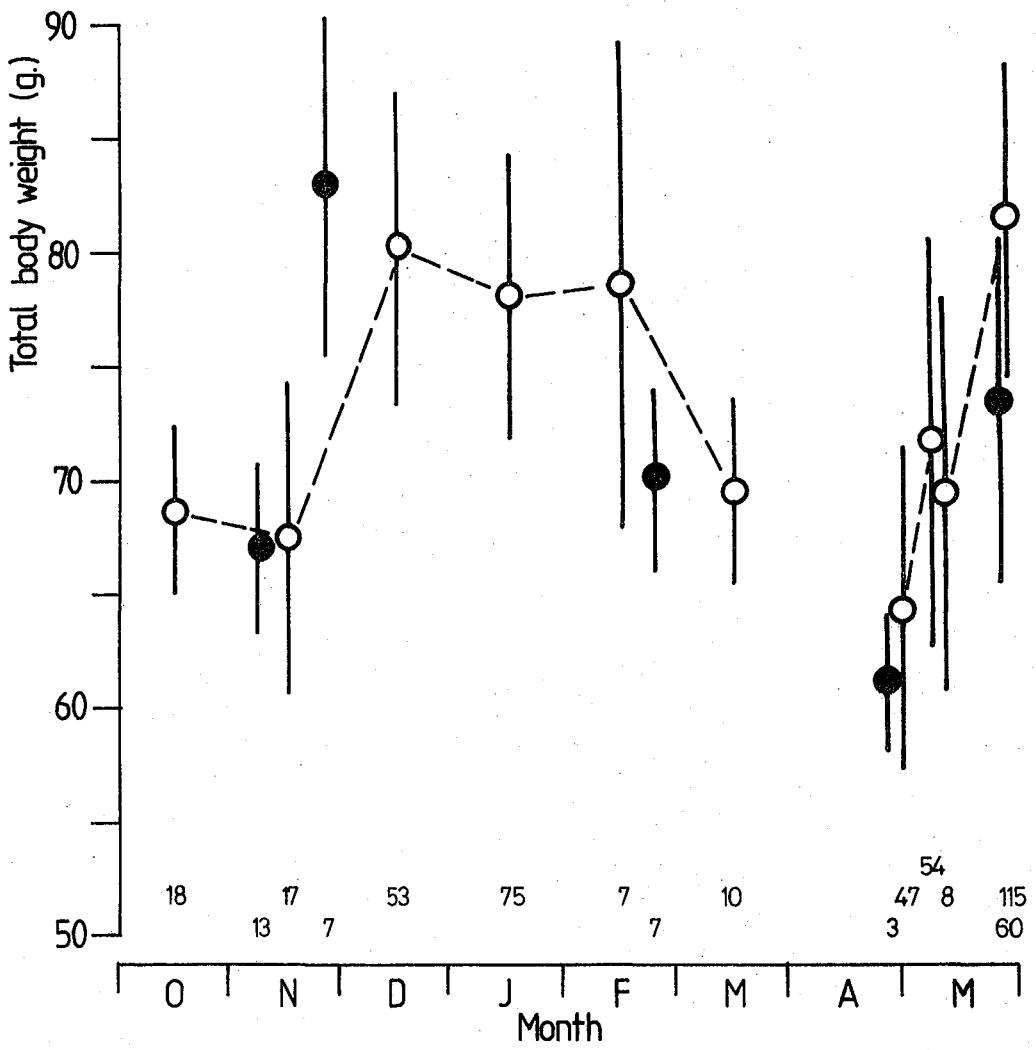

Figure 3: Total body weights of adult Ringed Plovers at Teesmouth (●), and at Morecambe Bay (o), from Clapham (1978). Points show the mean $\pm$ 1 standard deviation, plotted by month for Morecambe Bay and on date of capture for Teesmouth. Numbers indicate sample sizes.

Golden Plover, Pluvialis apricaria (L.)

Golden Plovers were collected at Lindisfarne primarily to examine changes in nutritional condition induced by severe weather. Most samples were from January and February 1978.

As Golden Plovers cannot be aged reliably on plumage characteristics in winter after November (Prater, Marchant & Vuorinen 1977), birds collected after November are treated as adults. Lipid indices (Table 7) averaged 20.5% in January and 24.5% in February. The difference was not significant ($t_{18} = 1.93$ $P > .10$). A first-year Golden Plover in early October also had a very high lipid index (21%). Golden Plovers had large pectoral muscles (>.3 SMV) (Table 8). Pectoral muscle size did not vary significantly between January and February (.323 $\pm$ .006 SMV (n = 15), ($t_{18} = 1.05$ $P > .10$). Pectoral muscles formed a high percentage of the total lean weight of Golden Plovers (Table 8), averaging 7.75% on 8 February 1978. Total lean weights did not change between January (182.2 $\pm$ 4.1 g. (n = 5)) and February (180.3 $\pm$ 3.6 g. (n = 15)), ($t_{18} = 0.339$ $P > .10$).

Grey Plover, Pluvialis squatarola (L.)

Fat Reserves

Only three Grey Plovers from north-east England have been analysed for nutritional condition. However it proved possible to estimate the lipid indices of adults from the weights of live birds caught at Teesmouth between 1975 and 1980, using methods in Appendix 2. Lipid indices rose to a peak in late December, before declining rapidly until at least the end of February (Figure 4). In mid-September a sample of moulting Grey Plovers carried an average of 8% fat

Table 7. Lipid indices of Golden Plovers from Lindisfarne

Date	n	Lipid index (%)
3.10.72*	1	21.0
19.01.78	5	20.6 ± 1.8
5.02.78	5	25.2 ± 2.1
8.02.78	10	24.2 ± 0.8

Values are mean ± 1 standard error.

* This bird was a first-year: all others were ~~adult~~. imaginable!

Table 8. Pectoral muscle size of Golden Plovers from Lindisfarne

Date	n	Pectoral muscle index	
		SMV	% LW
3.10.72*	1	.258	5.12
19.01.78	5	.307 ± .014	7.25 ± 0.23
5.02.78	5	.324 ± .006	7.67 ± 0.08
8.02.78	10	.323 ± .008	7.75 ± 0.14

Values are mean ± 1 standard error.

* This bird was a first-year: all others were ~~adult~~. imaginable!

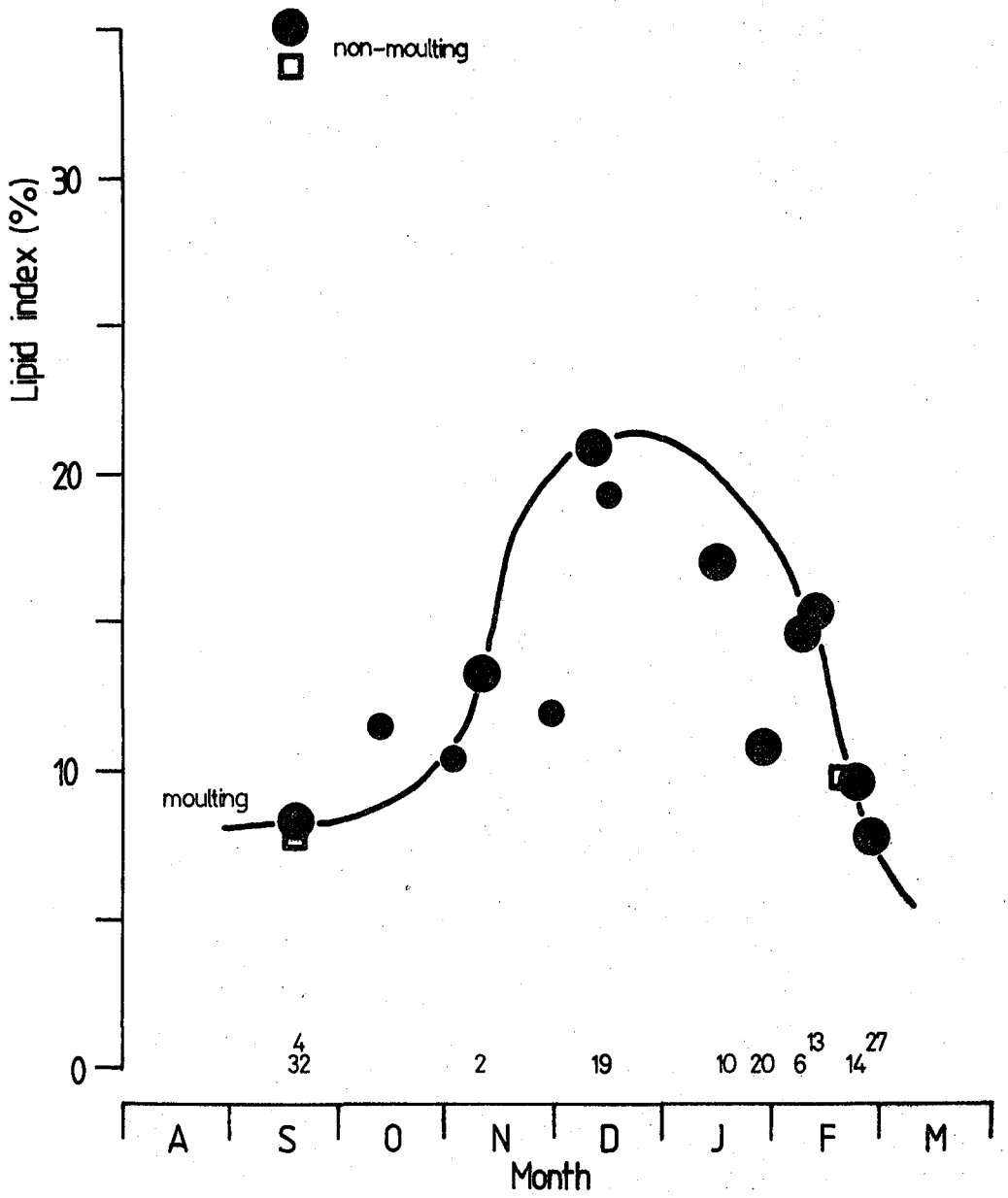

Figure 4: Lipid indices of adult Grey Plovers at Teesmouth. ● are mean values estimated from live birds (see Appendix 2), and □ are birds from which lipids were extracted. Small symbols are single birds. Numbers indicate sample sizes. Trend line fitted by eye.

(assuming lean weights were not lower during moult than later in the winter), whereas the lipid indices of non-moulting adults in the same catch averaged 35%. The non-moulting birds were probably accumulating fat for further migration, although some are known to have remained at Teesmouth for several weeks after capture, before departing (Dugan 1981a). Lipid indices avaraged 21% in mid-December, but this could be an underestimate of peak levels, since no Grey Plovers were caught in late December/early January when lipid indices may have been at their highest. The decline in lipid indices during late winter was rapid and by late February Grey Plovers carried only about 8% fat.

Pectoral Muscle Size

It was not possible to estimate pectoral muscle size from live Grey Plovers (see Methods) and so seasonal trends could not be examined in detail. Pectoral muscle size as a proportion of SMV was similar in the moulting and non-moulting adult in September (Table 9). The Grey Plover from late February had smaller pectoral muscles (.304 SMV) than the September birds, although muscle size was still large. In September the pectoral muscles of Grey Plovers formed a high percentage of total lean weight ($\bar{x}$ 6.32%).

Knot, *Calidris canutus* (L.)

Samples of Knots were collected from only two parts of the winter: mid-November to mid-December, and late January to early March, with most complete coverage during the 1977/78 winter.

Table 9. Pectoral muscle size of Grey Plovers at Teesmouth

Date	n	Pectoral muscle index	
		SMV	% Lean Wt.
18.9.78	2	.361 ± .011	6.32 ± 0.40
20.2.73	1	.304	5.94

Values are mean ± 1 standard error.

Fat Reserves

The pattern of the lipid indices of adult and first-year Knots (Figure 5) is consistent with lipid deposition occurring in early winter resulting in a mid-winter peak followed by a decline in late winter. In adults the increase in lipid index between mid- and late November is significant ($t_{10} = 2.511$ $P < .05$) although the data are from two different years and so could be a year-to-year difference. During late January and early February, the only period in which samples from different years can be compared, there were no significant between-year differences in lipid indices (Figure 5). First-year Knots followed a similar pattern to adults but had consistently higher lipid indices than adults during 1977/78 (difference between mean lipid index of adults and first-years, paired comparison $t_3 = 5.70$ $P < .02$). Lipid indices of both first-year and adult Knots were lower than expected on 9 December 1977. The reasons are discussed later. Lipid indices of adults average in excess of 15% at their mid-winter peak. During November and December 1977 the lipid indices of first-year Knots were significantly more variable than in February 1978 (variance ratios, November/February $F = 17.40$ $P < .02$, December/February $F = 6.28$ $P < .05$), but the variances of the lipid indices of adults were similar.

Pectoral Muscle Size

Pectoral muscle size as a proportion of standard muscle volume (Figure 6) increased slightly, but not significantly, during the winter (November - February) in both adults ($r_{43} = .155$) and first-years ($r_{16} = .235$). During one winter (1977/78) there was a stronger relationship in both adults ($r_{18} = .428$ $P < .10 > .05$) and first-years ($r_{14} = .495$ $P < .05$).

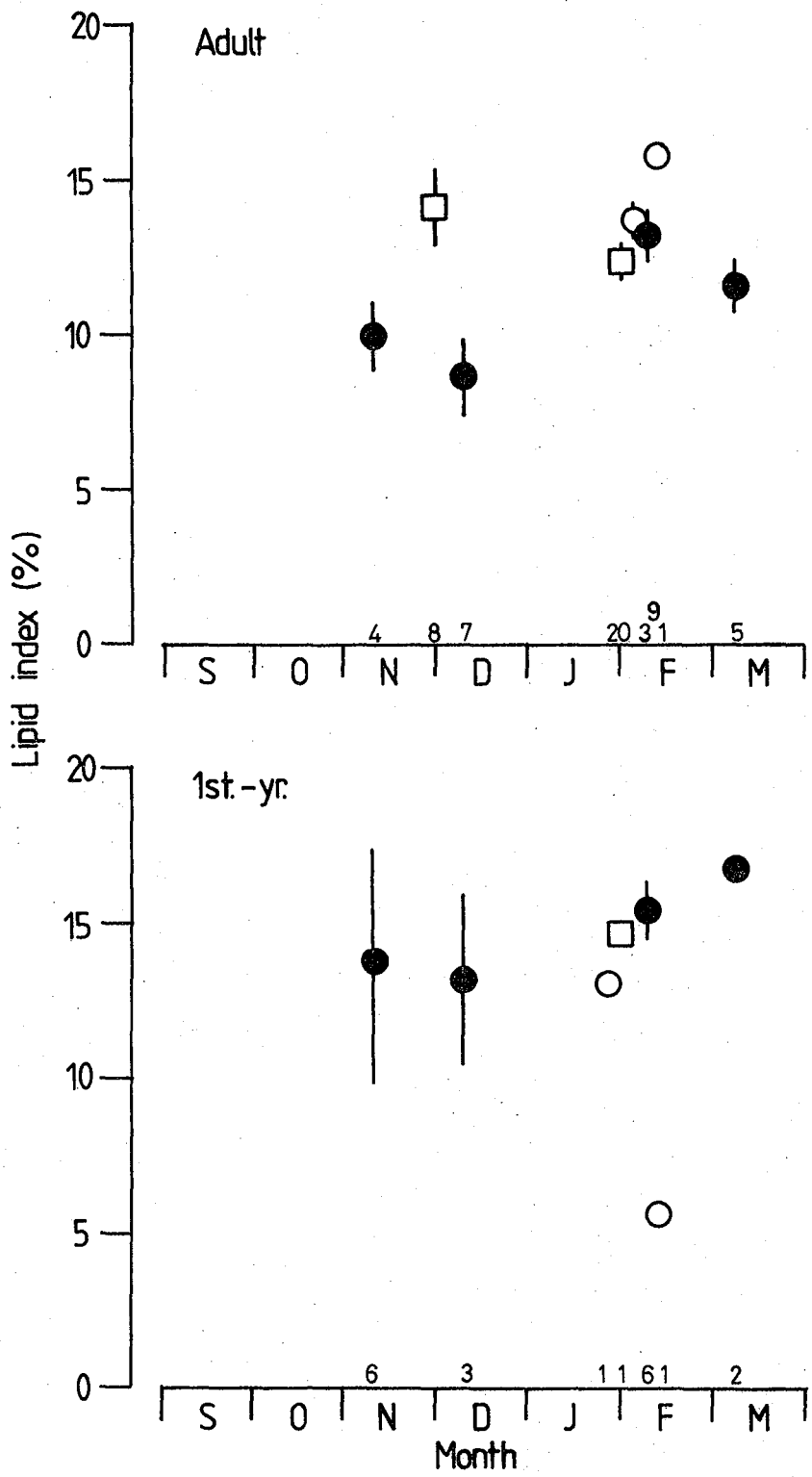

Figure 5: Lipid indices of Knots at Teesmouth. Values are the mean ± 1 standard error. Numbers indicate sample sizes. Symbols indicate different years: □ 1972/73, ■ 1975/76, ○ 1976/77, ● 1977/78.

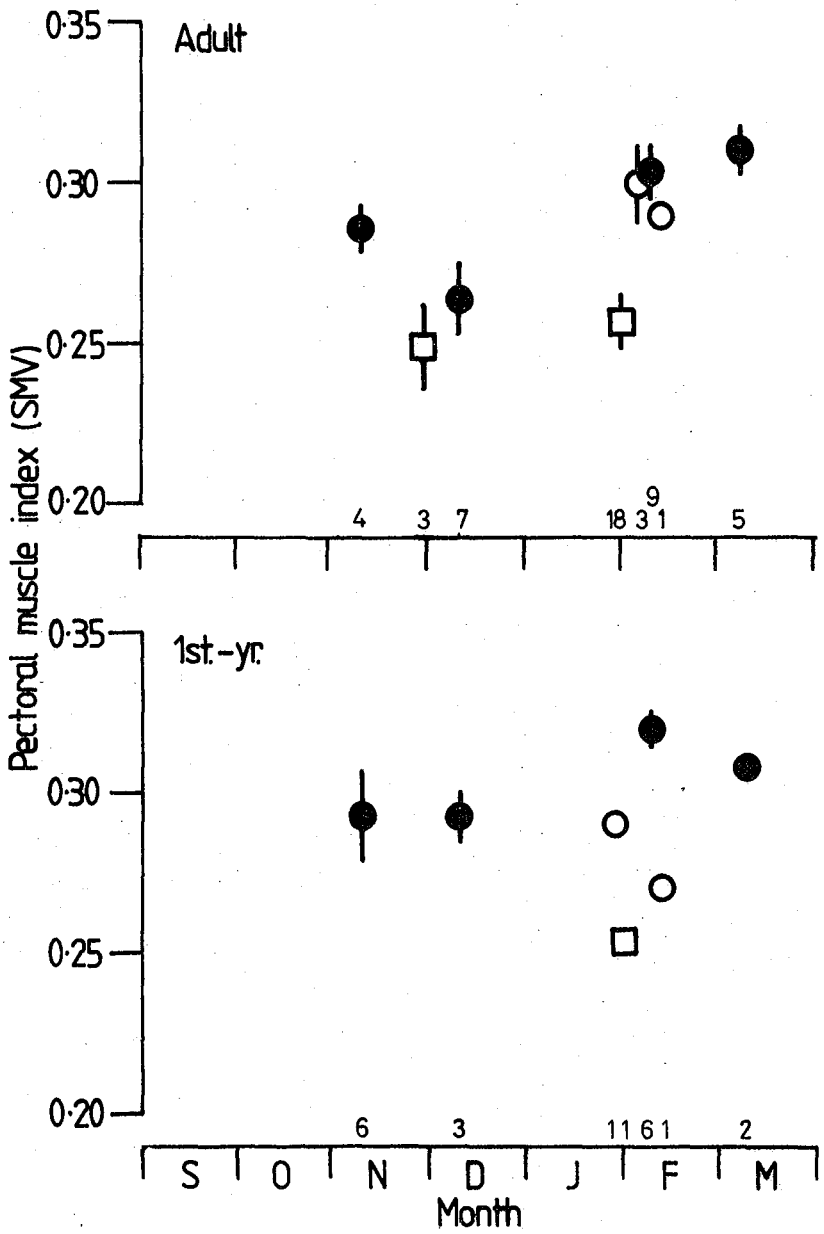

Figure 6: Pectoral muscle indices (SMV) of Knots at Teesmouth. Legend as Figure 5.

There is some evidence of between-year differences in adults since pectoral muscle size on 30 January 1973 was lower than on 5 February 1977 ($t_{19} = 3.03$ $P < .02$) and 9 February 1978 ($t_{25} = 3.92$ $P < .001$). However, pectoral muscle size was similar in February 1977 and 1978. The muscle sizes of the other sample taken during the 1972/73 winter, on 29 November 1972, were also low compared with those on 10 November 1977, although the difference is barely significant ($t_5 = 2.652$ $P < .10 > .05$). In March 1978 pectoral muscles were significantly larger than during the preceding winter (1977/78) in adults (winter $\bar{x}$ .286, March $\bar{x}$ .311, $t_{23} = 2.511$ $P < .05$), but not first-years (winter $\bar{x}$ .302, March $\bar{x}$ .307, $t_{16} = 0.291$ $P > .10$).

Pectoral muscle size as a percentage of total lean weight (Figure 7) also increased slightly during winter in adult and first-year Knots. In adults the percentage contributed to total lean weight by the pectoral muscles during 1977/78 was significantly less in both November (5.06% $t_{11} = 3.800$ $P < .02$) and December (5.04% $t_{14} = 3.321$ $P < .02$) than in February (5.60%), as was the index in March (5.22% $t_{12} = 4.008$ $P < .005$). The index did not change significantly in the first-year Knots during 1977/78. There were no significant between-year differences in adults. An age difference occurred only in March, when the pectoral muscles formed a larger proportion of total lean weight in first-years than adults (first-year 5.53%, adults 5.22%, $t_5 = 5.030$ $P < .02$).

Total Lean Weights

There was no evidence of marked seasonal changes in total lean weight during 1977/78 (Table 10), although individual lean

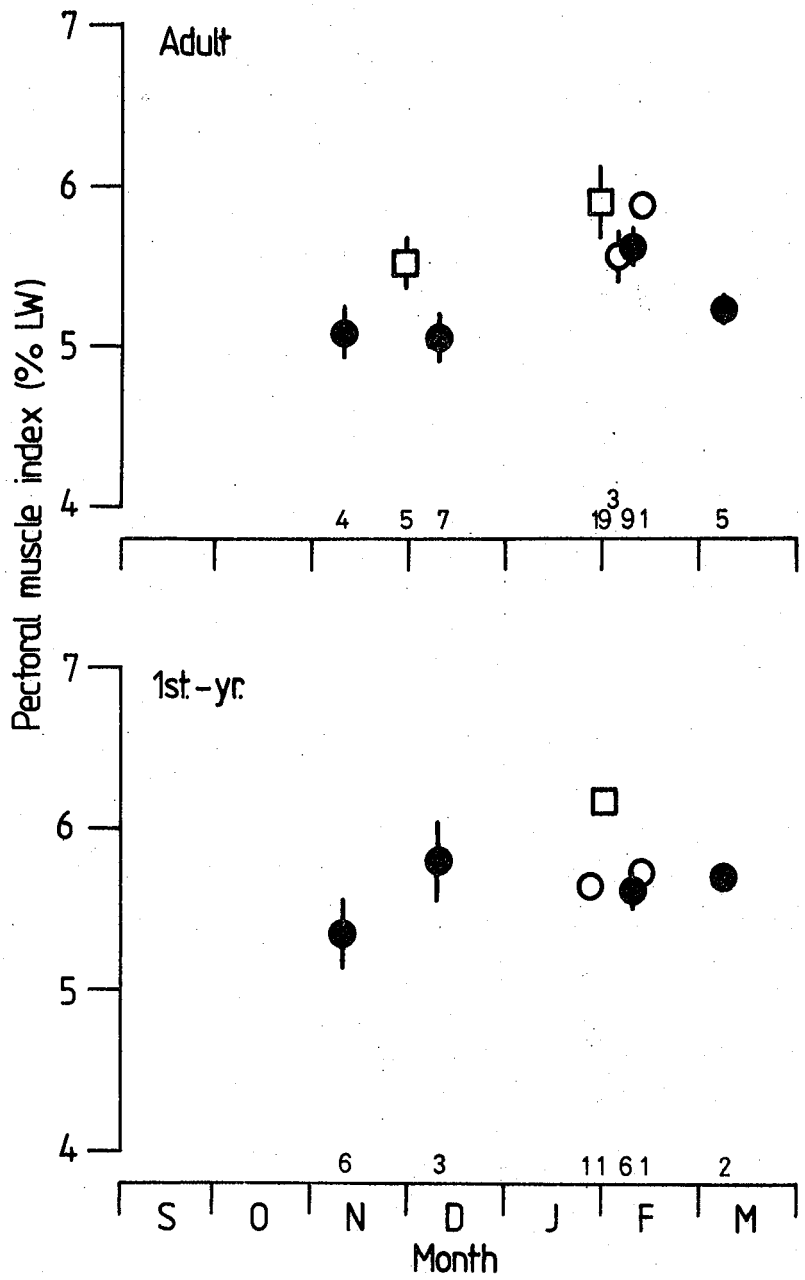

Figure 7: Pectoral muscle indices (% LW) of Knots at Teesmouth. Legend as Figure 5.

Table 10. Lean Weights (g.) of Knots at Teesmouth during the 1977/78 winter

	Adult		First-year	
	male	female	male	female
10 Nov. 1977	131.2 (1)	138.3 ± 3.9(3)	129.2 ± 2.0(3)	137.0 ± 7.0(3)
9 Dec. 1977	127.1 ± 0.9(3)	142.9 ± 3.4(4)	128.5 ± 7.4(2)	140.4 (1)
9 Feb. 1978	134.8 ± 3.5(4)	141.5 ± 1.8(5)	137.8 ± 3.6(3)	139.6 ± 6.2(3)
7 Mar. 1978		138.6 ± 1.2(5)		136.2 ± 0.6(2)

Figures are $\bar{x}$ - 1 s.e.(n)

weights differed greatly. Adult female Knots ($\bar{x}$ 140.4 g.) were heavier than adult males ($\bar{x}$ 131.5 g.), as were first-years (females $\bar{x}$ 138.1 g., males $\bar{x}$ 132.3 g.). In each sex, adults were heavier than first-years.

Sanderling, Calidris alba (Pallas)

Sanderlings use the coastal sandy beaches to the north and south of the Tees estuary. Almost all the small samples were from late winter and spring (February - May), and from several years (see Table 1).

Fat Reserves

In late winter the lipid indices of Sanderlings were high (Figure 8). The 26.4% lipid index of an adult Sanderling in early February was higher than any lipid index recorded in Dunlins during winter. Lipid indices of Sanderling during March were lower than in February. Mean lipid indices in both adults and first-years in March were 9.7%. Lipid indices increased in spring and by late May the lipid indices of adult Sanderlings averaged 27%. However there was considerable variation in these late May lipid indices with three birds carrying 9 - 15% fat, and three carrying 37 - 47% fat. These latter were the highest values recorded in this study. Total body weights of Sanderlings at Teesmouth (Figure 9) confirm this decline in fat reserves in late winter, followed by a rapid increase in mean weight in spring. Total body weight gradually increases during autumn and early winter.

Pectoral Muscle Size

Pectoral muscle size as a proportion of SMV (Figure 10a) in February/March was similar in adults ($\bar{x}$ .270 SMV) and

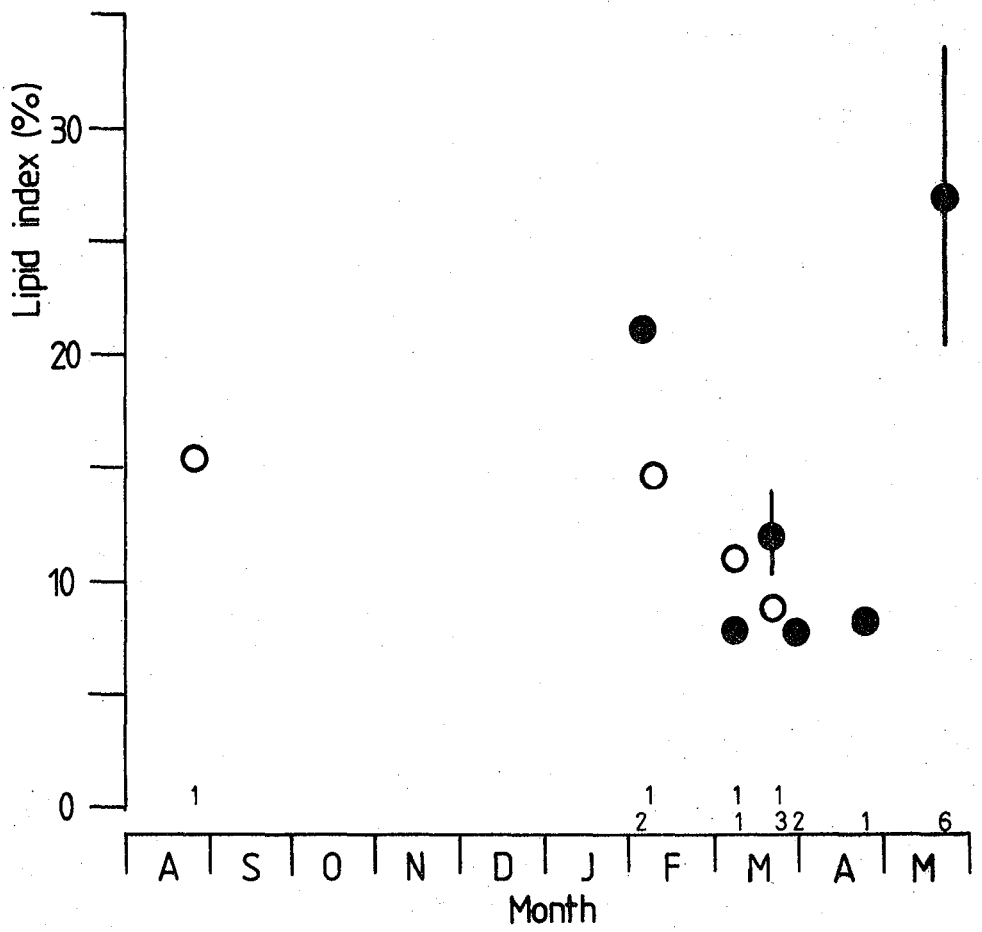

Figure 8: Lipid indices of adult (•) and first-year (o) Sanderlings at Teesmouth. Points show the mean ± 1 standard error. Numbers indicate sample sizes.

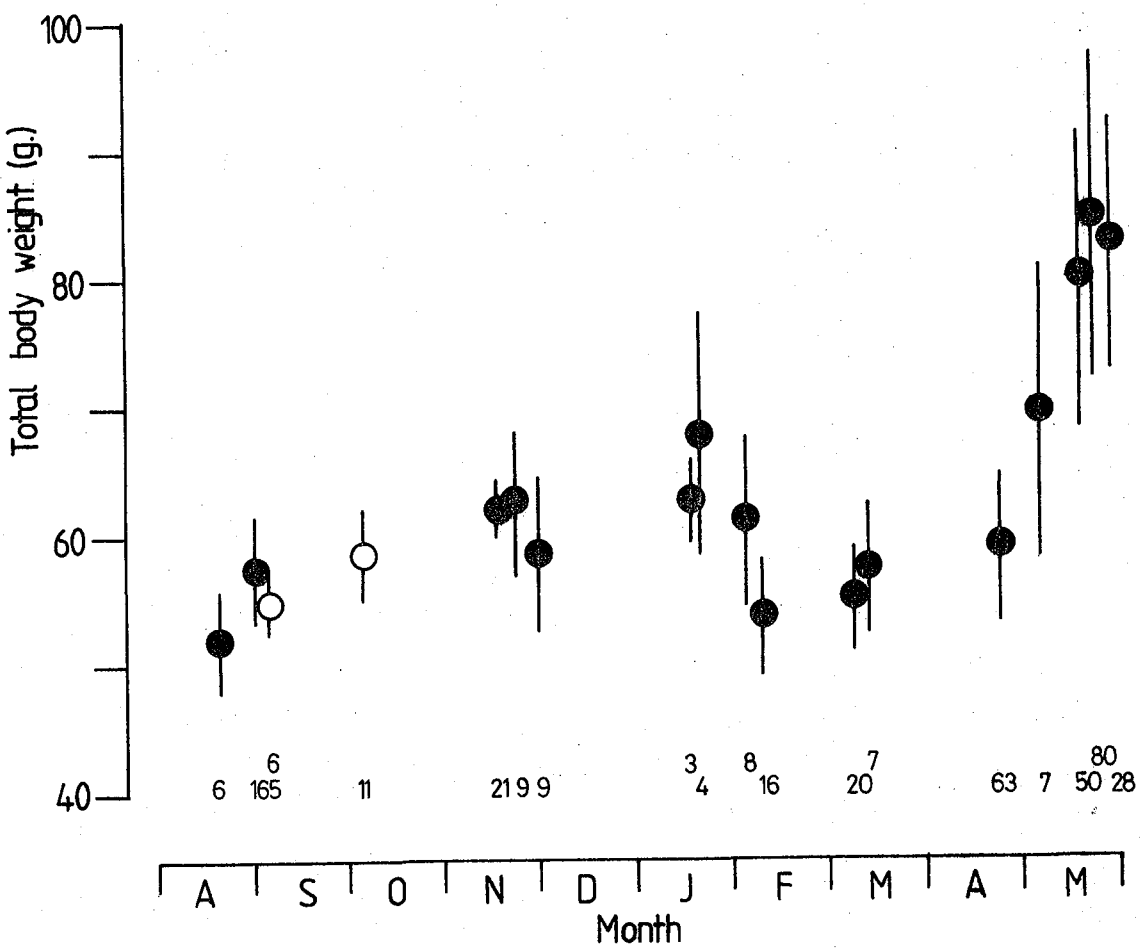

Figure 9: Total body weights of adult Sanderlings at Teesmouth. Points show the mean ± 1 standard deviation. Open circles are moulting birds. Numbers indicate sample sizes.

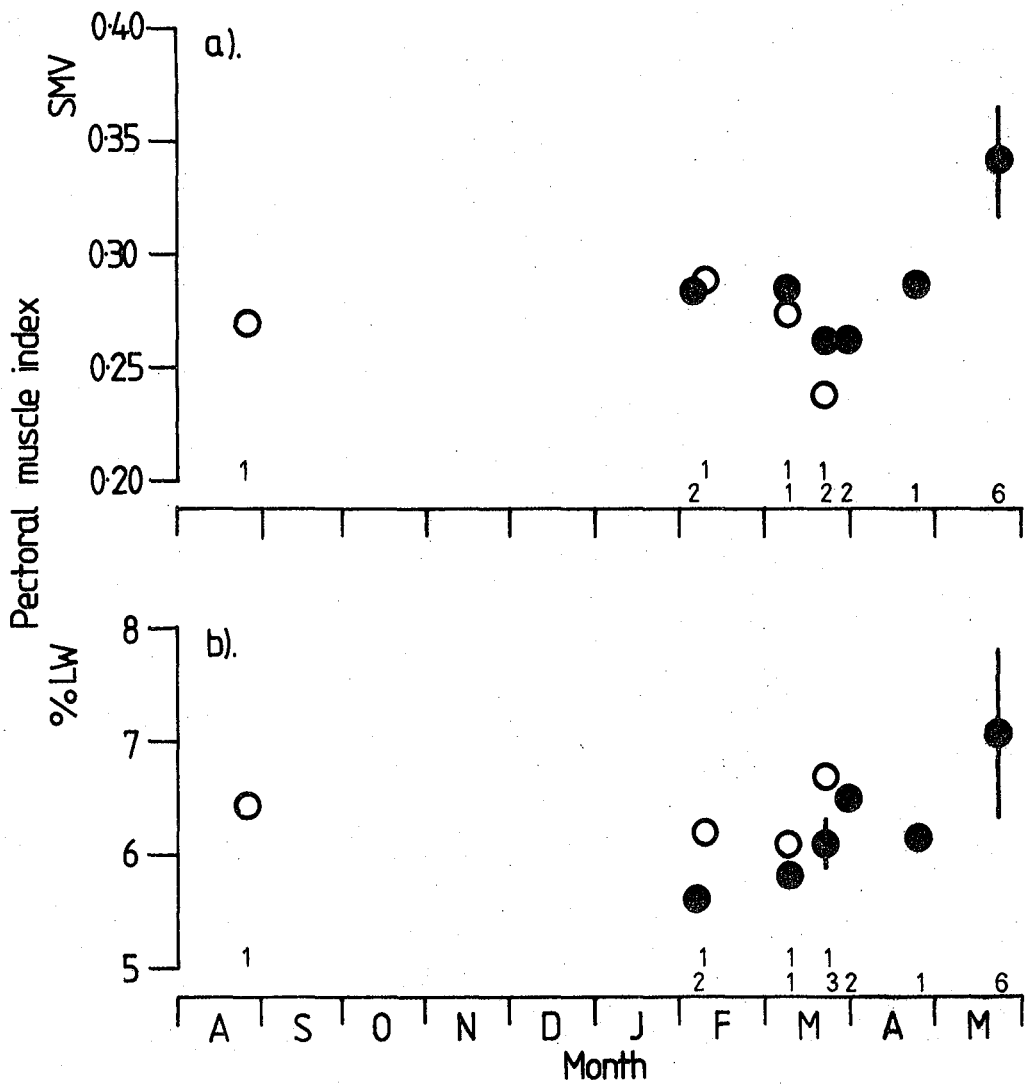

Figure 10: Pectoral muscle indices of Sanderlings at Teesmouth a) SMV, and b) % LW. Legend as Figure 8.

first-years ($\bar{x}$ .265 SMV). The increase in pectoral muscle size between March and May, to average .339 SMV by late May, was significant (Spearman r_{12} = .717 $P < .01$). One Sanderling in late May had extremely large pectoral muscles (.451 SMV). This bird also had the highest recorded lipid index (47%) and pectoral muscle size and lipid index were strongly correlated in late May (see Figure 21).

Pectoral muscle size as a percentage of total lean weight (Figure 10b) changed seasonally like the SMV index, and averaged 6.0% in late winter. By late May, pectoral muscles had increased to 7.0% of total lean weight, although the difference between winter and spring was not significant due to the high variance of the late May sample. There was a significant increase in total lean weight between late winter and late May (Spearman r_{13} = .526 $P < .05$).

Dunlin, Calidris alpina (L.)

Samples of Dunlins from Teesmouth were available from six non-breeding seasons between 1971 and 1979, the most complete being 1977/78. All Dunlins sampled were of the nominate C.a. alpina race, which occurs at Teesmouth on spring and autumn passage in addition to forming the over-wintering population.

Fat Reserves

Lipid indices between September and May are shown for adults in Figure 11 and first-years in Figure 12. There were no consistent interyear differences. Moulting adults in mid-September 1977 had a mean lipid index of only 2.75%, significantly lower than one month later (t_{10} = 6.871 $P < .001$). Lipid indices rose during the autumn from a mean of 6% in

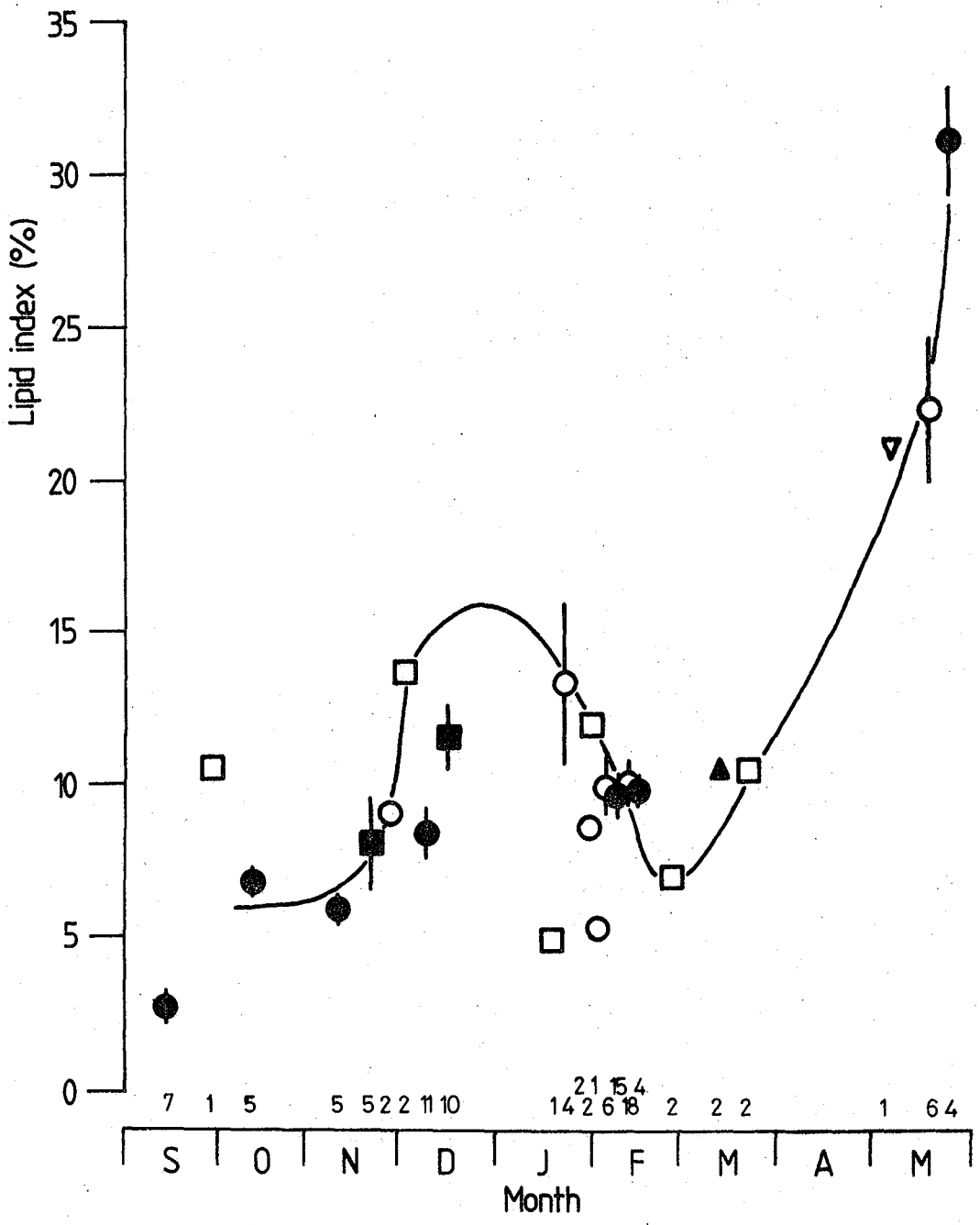

Figure 11: Lipid indices of adult Dunlins at Teesmouth. Symbols indicate different winters: ▲ 1971/72, □ 1972/73, ■ 1975/76, ○ 1976/77, ● 1977/78, ▽ 1978/79. Each point shows the mean ± 1 standard error. Numbers indicate sample sizes. Trend line fitted by eye, excluding samples with smaller lipid indices than normal (see later).

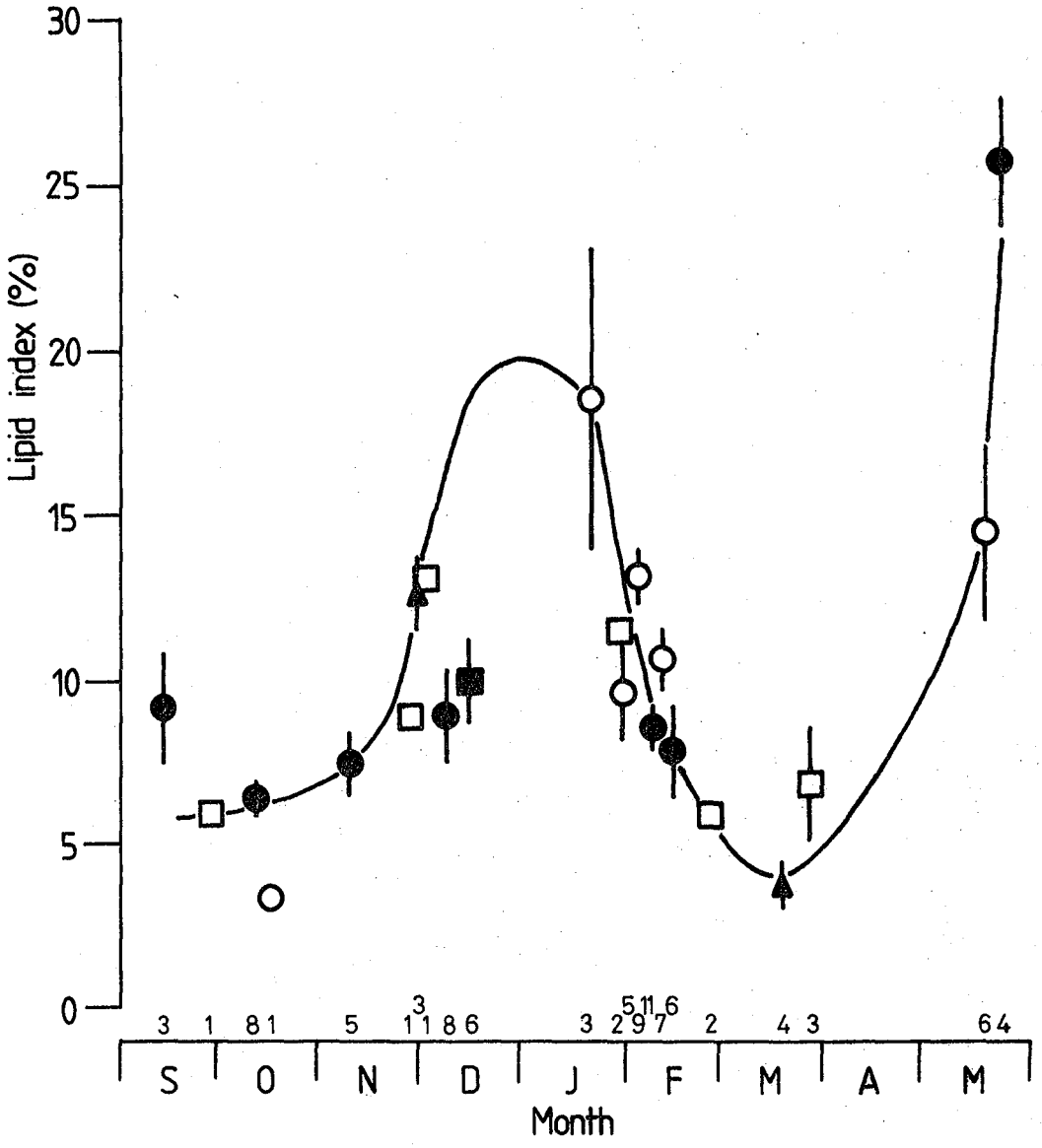

Figure 12: Lipid indices of first-year Dunlins at Teesmouth. Legend as Figure 11.

October to 13.5% in early December. No Dunlins were collected in late December or early January, so although fat levels probably continued to increase during December, it was not possible to establish peak levels, although they probably averaged at least 15% of total body weight by late December. The highest individual lipid index recorded in midwinter was 20.3%. Lipid indices declined after midwinter, averaging 7% by the end of February, before increasing rapidly again in spring, between March and May to an average of 31% by late May. This spring increase is highly significant (Spearman $r_{15} = .852$ $P < .001$). Two samples of adult Dunlins collected on 16 December 1975 and 9 December 1977 had unexpectedly low lipid indices (means of 11.7% on 16 December 1975 and 8.6% on 9 December 1977).

First-year Dunlins (Figure 12) showed some differences in lipid index from adults. In September 1977, first-years (in body but not wing-moult) had significantly higher lipid indices than adults ($t_8 = 4.373$ $P < .01$), but the mean lipid index of 6% in October (after moult) was similar to that of adults. The total body weights of several individual first-year Dunlins in autumn increased rapidly (Figure 13). Much of this weight increase would have been fat stored for further migration. Two of these migrant first-year birds maintained a steady weight for over a month before rapidly storing fat. Fat reserves, as in adults, increased during early winter to reach a mean of 12.5% by early December. As for adults, peak midwinter lipid indices could not be established firmly, but the mean peak level was probably higher than in adults, at around 20% (Figure 12). Peak lipid indices probably occurred

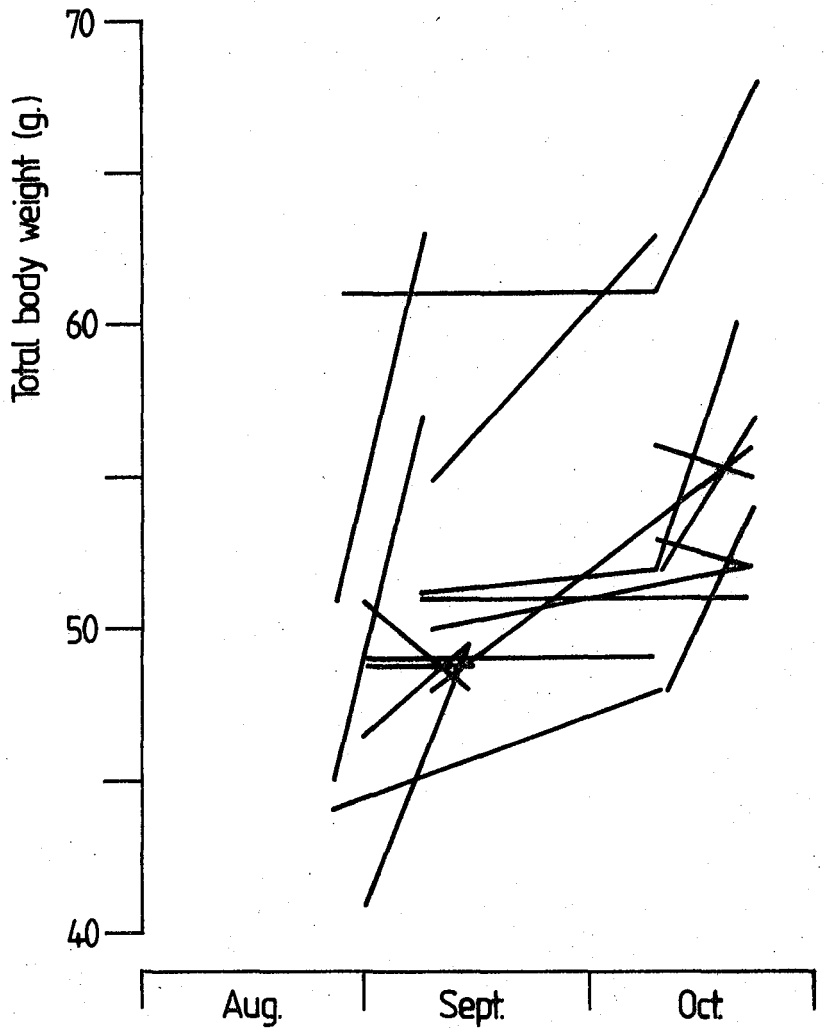

Figure 13: Within-year changes in the total body weight of first-year Dunlins weighed at least twice during autumn (August-October) at Teesmouth. Each line joins the weights of one individual.

in late December. Highest midwinter lipid indices were found in two individuals carrying 24.3% and 21.4% fat on 23 January 1977, both these values being higher than the maximum adult midwinter lipid index.

The lipid indices of first-year Dunlins declined between January and March, as found also in adults, but first-years had higher lipid indices in January and early February: on 5 February 1977 the difference was significant (adult 10.0 $\pm$ 0.9, first-year 13.1 $\pm$ 0.8; $t_{13} = 2.67$ $P < .02$). By mid-February lipid indices were similar in both age-classes, but the decline in the lipid indices of first-year birds continued until late March, averaging only 3.7% on 21 March 1972, which was significantly lower than in adults five days earlier ($t_4 = 5.63$ $P < .01$). Spring fattening by first-years started later than by adults, and in both May 1977 and May 1978 first-years carried lower lipid indices than adults, although variances are high and the differences not significant. The spring increase to a mean lipid index of 26% by late May was highly significant (Spearman $r_{17} = 0.83$ $P < .001$).

Pectoral Muscle Size

Pectoral muscle size as a proportion of SMV (Figure 14) changed little between October and February (adults, $r_{87} = -.0209$ $P > .10$; first-years, $r_{73} = -.0571$ $P > .10$), and there were no consistent inter-year differences within either age-class. Further statistical comparisons are given in Tables 11 and 12. However, in September, during moult, both adult and first-year Dunlins had smaller pectoral muscles than during the winter. Adults in September 1977 had significantly smaller pectoral muscles than one month later. Additionally, pectoral muscles in September 1977 were significantly smaller than during

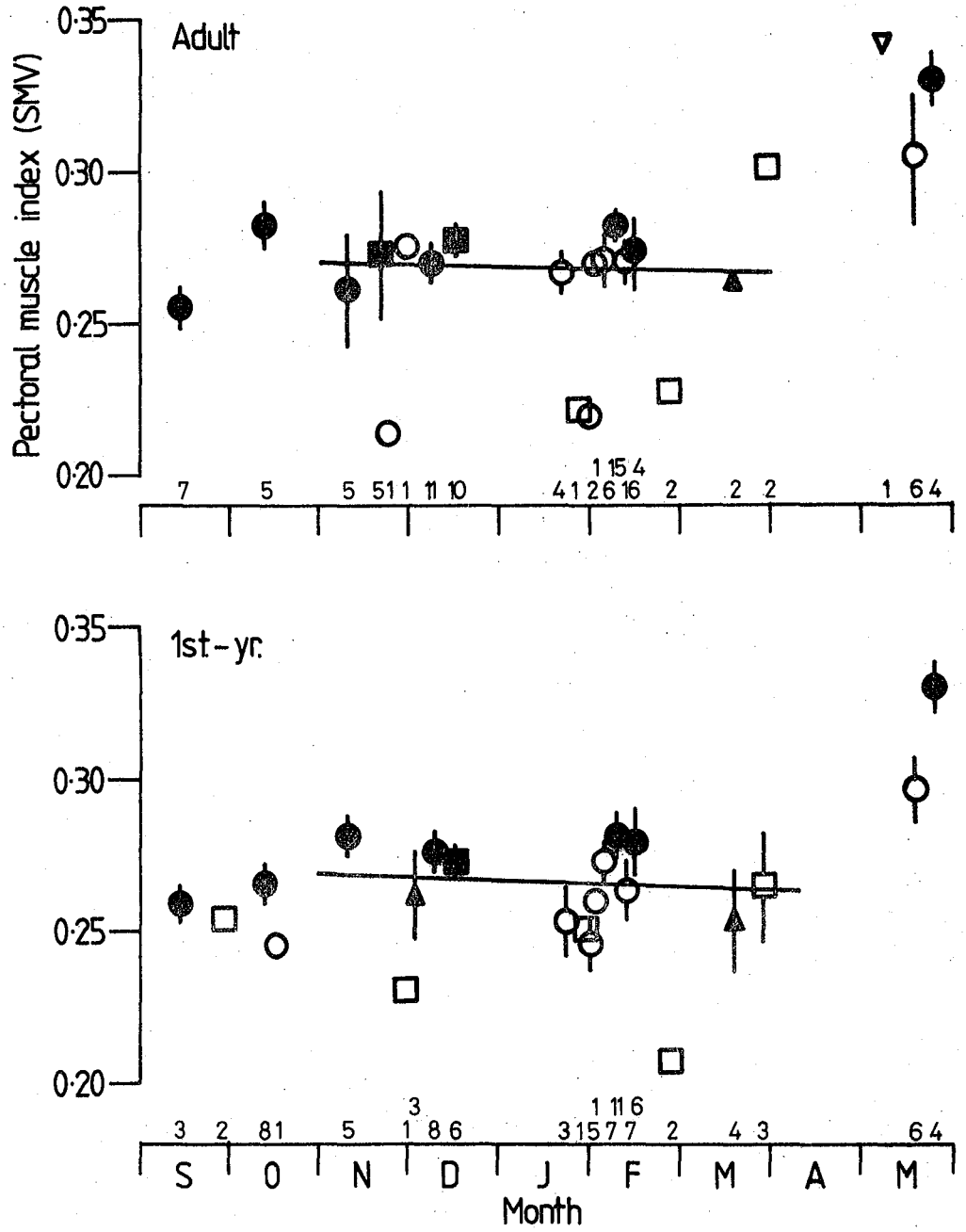

Figure 14: Pectoral muscle indices (SMV) of adult and first-year Dunlins at Teesmouth. Legend as Figure 11. Solid lines show least-squares regressions on individual birds during winter (October - February).

winter 1977/78 in both adults and first-years. The pectoral muscle size of first-years in October did not differ from the winter level. There was no age-related difference in pectoral muscle size during the winter. In spring, pectoral muscle size (SMV) increased significantly between March and May in both adults (Spearman $r_{15} = 0.5125$ $P < .05$) and first-years (Spearman $r_{17} = 0.7328$ $P < .01$). Although the onset of the spring increase is probably later in first-years than adults (Figure 14), pectoral muscle sizes were similar by late May (Table 12).

The second index of pectoral muscle size - lean dry pectoral muscle as a percentage of total lean weight - underwent similar seasonal changes to the SMV index (Figure 15). The index showed no significant change during the winter (October - February), with pectoral muscles averaging 5.75% of total lean weight in both age-classes. In Spring (March - May), pectoral muscles contributed an increasing proportion of total lean weight (Table 11). There were no age differences during winter or in May (Table 12).

In September the pectoral muscle index (% LW) showed a different pattern to that described for the SMV index. The percentage contributed to total lean weight by the pectoral muscles in September 1977 did not differ from the 1977/78 winter level in adults, but formed a significantly higher percentage of the total lean weight of first-years (Table 11). By October the percentage had reached its winter level. Since the pectoral muscles of first-year Dunlins were smaller in September than in the winter (Figure 14), it follows that the total lean weights of first-years must have been very low in September. Total lean weights are described below.

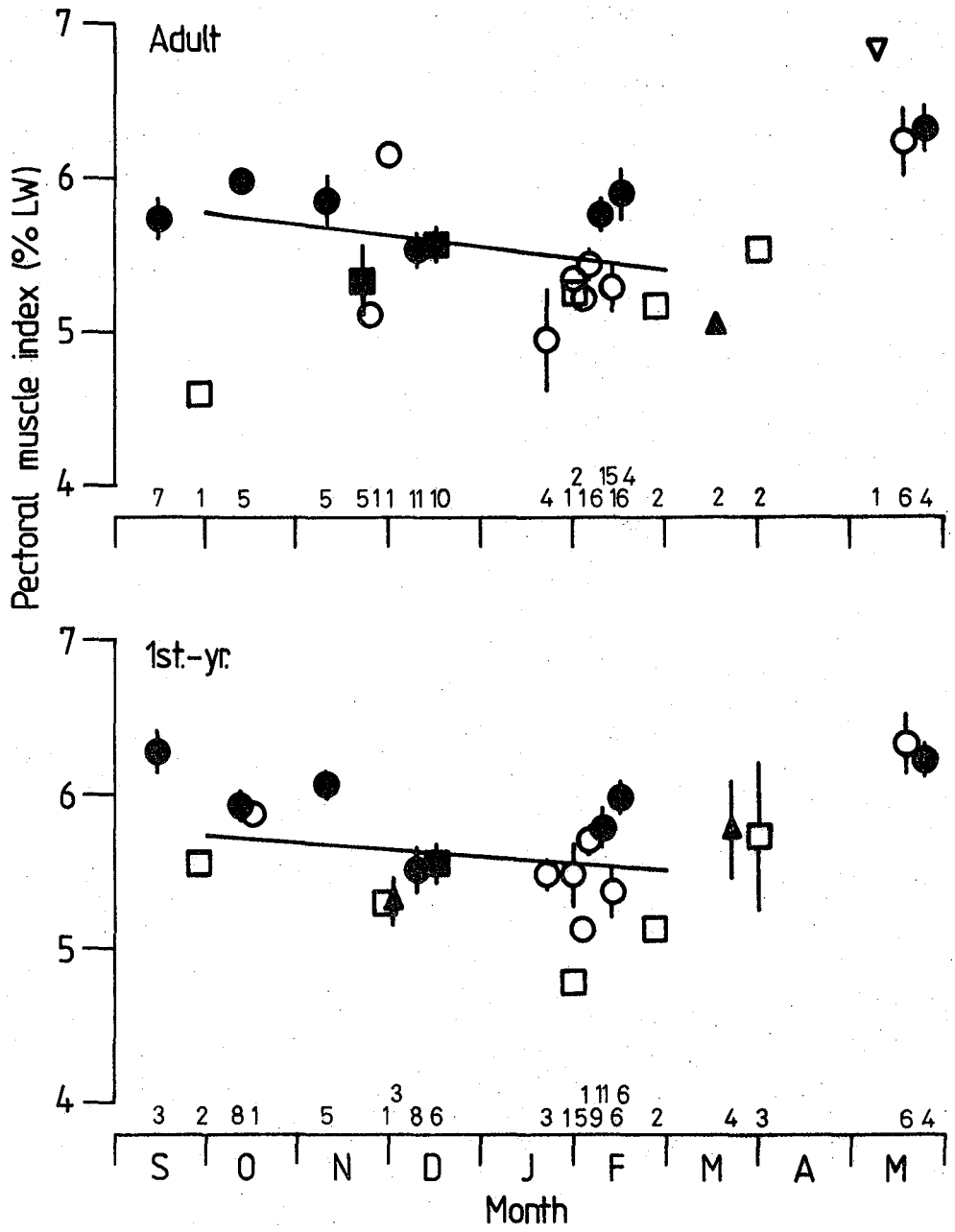

Figure 15: Pectoral muscle indices (% lean weight) of adult and first-year Dunlins at Teesmouth. Legend as Figure 11. Solid lines show least-squares regressions on individual birds in winter (October - February).

Table 11. Seasonal differences in the pectoral muscle size of Dunlins

	12 October 1977	14 September 1977	Winter 1977/78
Pectoral muscle index (SMV)			
Adults	.282 ± .017 (5)	.255 ± .006 (7)	.273 ± .003 (40)
	$t_{10} = 2.77$ $P < .02$	$t_{45} = 2.68$ $P < .002$	
First-years	.266 ± .017 (8)	.259 ± .004 (3)	.277 ± .003 (38)
	$t_{9} = 0.37$ $P > .10$	$t_{39} = 3.60$ $P < .01$	
Pectoral muscle index (% LW)			
Adults	5.97 ± 0.05 (5)	5.74 ± 0.13 (7)	5.73 ± 0.06 (40)
	$t_{10} = 1.34$ $P > .10$	$t_{45} = 0.07$ $P > .10$	
First-years	5.92 ± 0.07 (8)	6.27 ± 0.12 (3)	5.81 ± 0.05 (38)
	$t_{9} = 2.64$ $P < .10 > .05$	$t_{39} = 3.62$ $P < .01$	

Values are mean ± 1 standard error (sample size).

Table 12. Age differences in the pectoral muscle size of Dunlins

	Pectoral muscle size (SMV)		Pectoral muscle size (% LW)	
	Adults	First-years	Adults	First-years
Winter 1977/78	.273 ± .003 (40)	.277 ± .003 (38)	5.73 ± 0.06 (40)	5.81 ± 0.05 (38)
	d_{76} = 1.11 P > .10		d_{76} = 0.98 P > .10	
18 May 1977	.303 ± .021 (6)	.296 ± .010 (6)	6.22 ± 0.22 (6)	6.32 ± 0.18 (6)
	t_{10} = 0.30 P > .10		t_{10} = 0.28 P > .10	
24 May 1978	.329 ± .008 (4)	.330 ± .007 (4)	6.31 ± 0.15 (4)	6.22 ± 0.07 (4)
	t_{6} = 0.04 P > .10		t_{6} = 0.58 P > .10	

Values are mean ± 1 standard error (sample size).

Total Lean Weights

Total lean weights were very variable, and because Dunlins are sexually dimorphic, males and females in each age-class were analysed separately (Figure 16). During winter (October- February) there were indications of a small, but not significant, overall increase in total lean weight. The data are also consistent with a peak in lean weight in midwinter followed by a gradual decline, but this pattern cannot be confirmed. In spring, total lean weight increased in all age- and sex-classes, although this increase was significant only in first-year females (Spearman $r_9 = 0.76$ $P < .05$). In the 1977/78 non-breeding season, total lean weights of both adult and first-year males were significantly higher in May than during the winter (Table 13).

First-year female Dunlins had significantly lower total lean weights in September 1977 than in either October 1977 ($t_9 = 3.27$ $P < .01$) or during the whole of the 1977/78 winter (Table 13). Adult females followed the same trends, but differences were not significant. No males were collected in September.

There is evidence of a further increase in total lean weight between November and December (Figure 16), since the lean weights of adult females increased significantly in 1975 ($t_8 = 2.98$ $P < .02$), as did first-year females in 1977 ($t_6 = 6.43$ $P < .001$). Other changes in lean weights followed the same trend. The high total lean weights in December were not due to differences in body size, since bill-lengths - a good estimator of body size (Appendix 2) - were not significantly different within an age- or sex-class between November and December. None of the bill-length differences

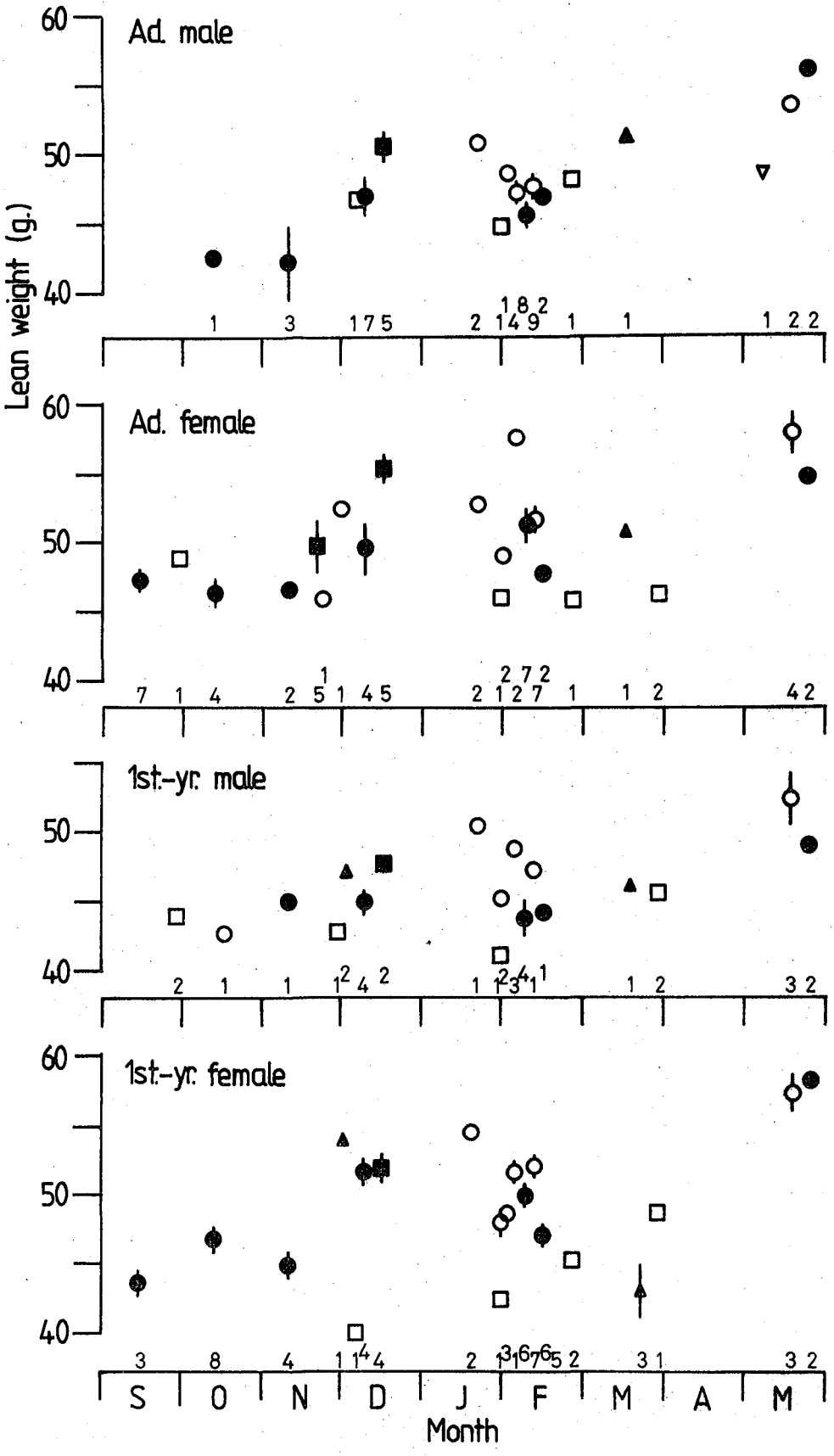

Figure 16: Total lean weights of Dunlins at Teesmouth. Legend as Figure 11.

Table 13. Total lean weights (g.) of Dunlins during 1977/78

	Adults		First-years	
	Male	Female	Male	Female
September		47.13 ± 0.51 (7)		43.52 ± 0.54 (3)
October - February	45.53 ± 1.58 (22)	48.86 ± 0.76 (19)	44.26 ± 0.61 (10)	47.97 ± 0.52*** (28)
May	55.92 ± 3.05** (2)	54.76 ± 2.76 (2)	48.72 ± 0.10*** (2)	58.14 ± 3.08** (2)

Values are mean ± 1 standard error (sample size).

Significant differences (Student's t-tests): ** $P < .01$, *** $P < .001$

can account for more than a 1 g. difference in total lean weight. Seasonal changes in total lean weight are examined in further detail in Paper 3.

Water Content

Water content, expressed as a percentage of total lean weight, remained constant between October and February (adults, $r_{56} = -.064$ $P > .10$; first-years, $r_{33} = .095$ $P > .10$). The mean water contents of adults (67.54%) and first-years (67.50%) were very similar during winter.

Bar-tailed Godwit, Limosa lapponica (L.)

Seasonal changes in the nutritional condition of Bar-tailed Godwits at Lindisfarne have been detailed previously by Evans and Smith (1975). Some further Godwits were collected in 1977 and 1978, primarily to examine changes in nutritional condition attributable to periods of severe weather (see Paper 2). These samples were collected between mid-January and early March, a period from which Evans and Smith (1975) had few samples, and can be used (a) to examine further the year to year consistency in levels of nutritional condition, and (b) to provide more complete information on the nutritional condition of Godwits in late winter.

Fat Reserves

Lipid indices of Godwits collected in 1977 and 1978, in comparison with Evans and Smith's (1975) values, are shown in Figure 17. In mid-January 1978 two samples of adults had mean lipid indices of 10.4% and 10.9%, very similar to the 10.8% lipid index found by Evans and Smith (1975) in adults in mid-January. Mean lipid indices of first-year Godwits in January 1978 (9.7% and 7.7%) also compared well with 8.0%

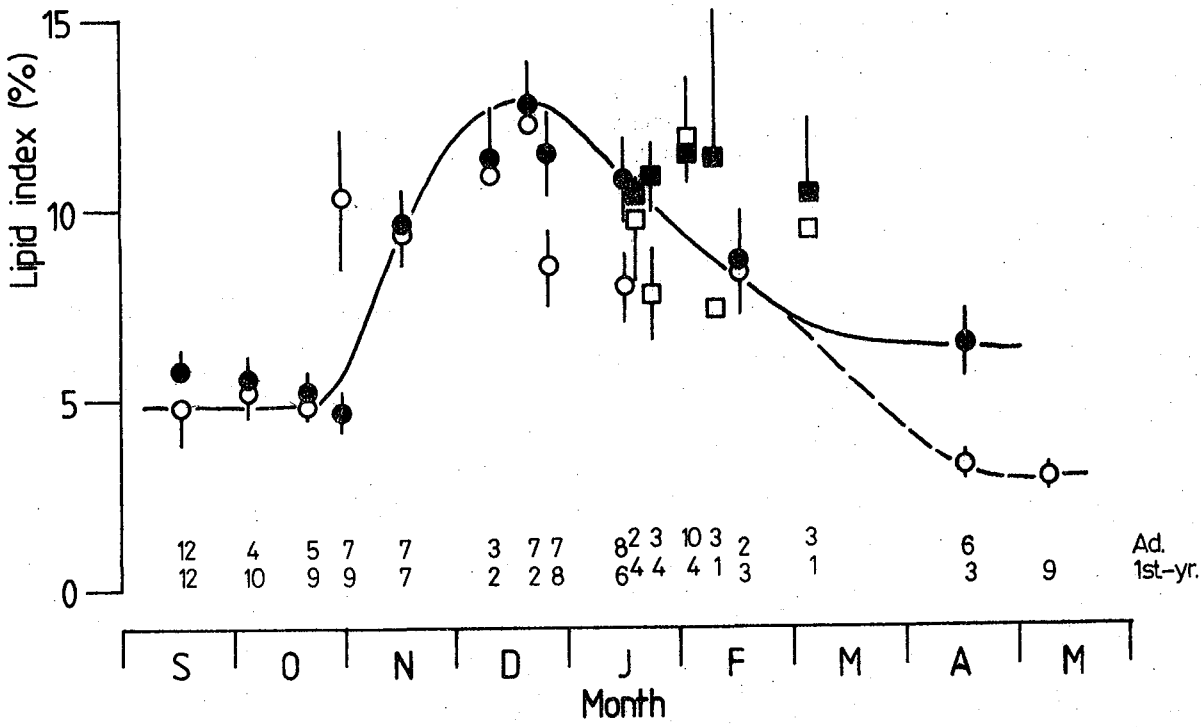

Figure 17: Lipid indices of Bar-tailed Godwits at Lindisfarne. Points show the mean ± 1 standard error. Open symbols are first-years, solid symbols are adults, for 1970-75 (○ ●) from Evans and Smith (1975), and 1977 and 1978 (□ ■). Numbers indicate sample sizes. Trend lines for adults (——) and first-years (- - -) from Evans and Smith (1975), fitted by eye.

in earlier years. None of the differences between adults and first-years or between years within an age-class in January were significant (Student's t, all $P > .05$). In early February and early March in recent years the lipid indices of adults were consistently, but not significantly, higher than in Evans and Smith's mid-February samples, suggesting that the lipid indices of adults declined less steeply after the December peak of 13% than shown by Evans and Smith (1975), and were maintained at about 10% until early March. First-year Godwits in February and March tended to have lower lipid indices than adults (Figure 17), but the differences were not significant.

Pectoral Muscle Size and Total Lean Weights

In 1977 and 1978 Pectoral muscle size as a proportion of SMV (Figure 18a) closely followed the seasonal pattern of muscle size found by Evans and Smith (1975), in which pectoral muscle size of adults remained steady throughout the winter with a mean index of .295 SMV. During January - March 1977 and 1978, adult Godwits had a mean pectoral muscle size of .291 SMV. Evans and Smith (1975) found that first-year Godwits had significantly smaller pectoral muscles than adults during autumn and early winter, but that the pectoral muscles had grown to reach adult size by February. The absence of age differences in pectoral muscle size during mid-winter is confirmed by data from 1977 and 1978. Of four samples taken in late January and early February, the pectoral muscles of first-year Godwits were slightly larger than those of adults in three samples, and smaller in one. Age differences were not significant (Table 14) and pectoral muscles of first-years had grown to adult size by mid-January.

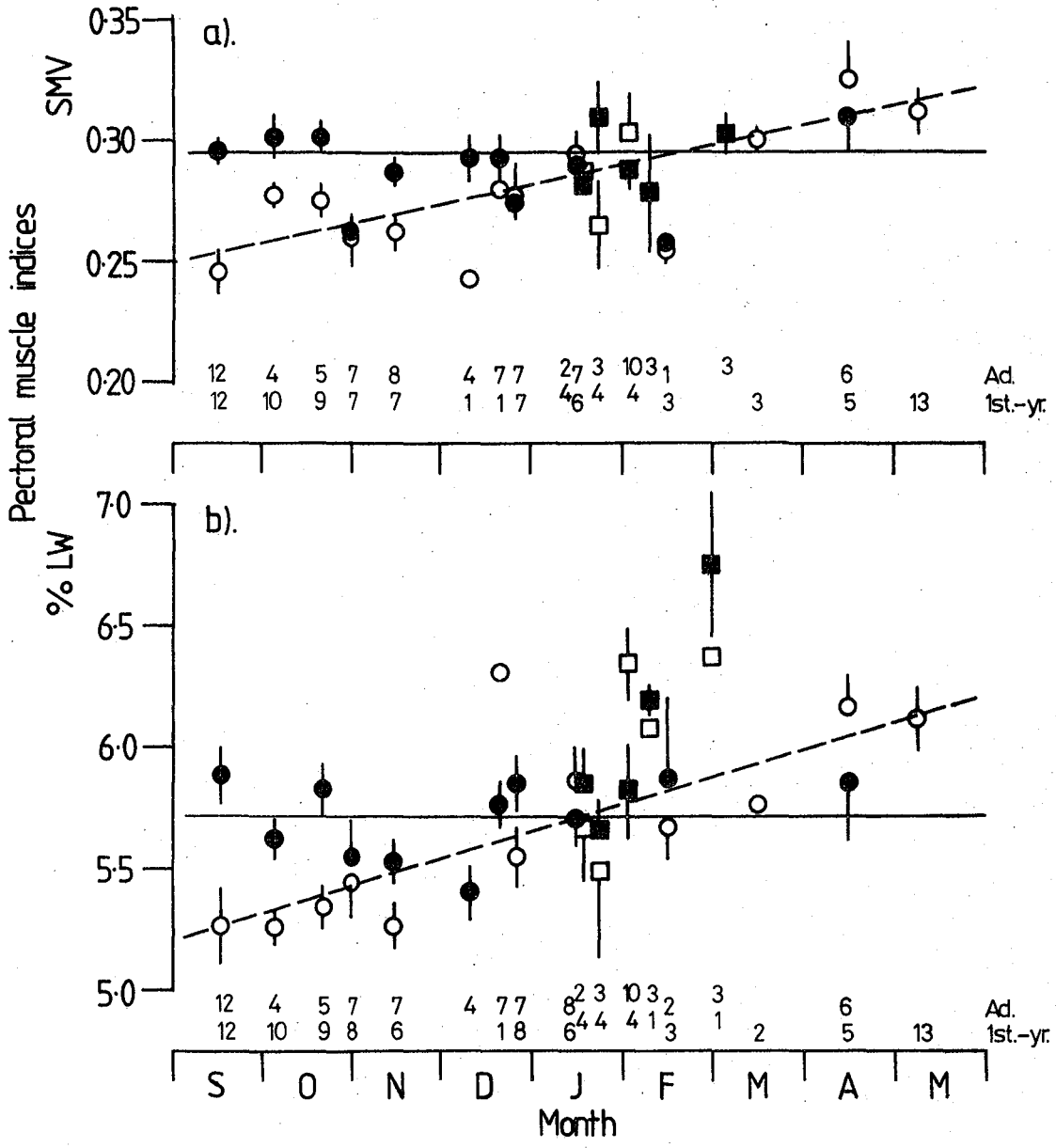

Figure 18: Pectoral muscle indices a) SMV, b) % Lean weight, of Bar-tailed Godwits at Lindisfarne. Legend as Figure 17. Least-squares regressions for adults (——) and first-years (- - -) from Evans and Smith (1975).

Table 14. Comparison of the pectoral muscle size (SMV) of adult and first-year Bar-tailed Godwits at Lindisfarne in January and February 1977 and 1978.

Date	Adult	First-year	Student's t (Age-difference)	
16 January	.284 ± .020 (2)	.286 ± .009 (4)	0.09	n.s.
22 January	.309 ± .014 (3)	.265 ± .017 (4)	2.00	n.s.
2 February	.287 ± .007 (10)	.302 ± .033 (4)	0.44	n.s.
9 February	.278 ± .024 (3)	.296 (1)		

Figures are mean ± 1 standard error (sample size).

Pectoral muscle size as a percentage of total lean weight showed a similar seasonal pattern (Figure 18b), with the pectoral muscles of adults averaging 5.7% of total lean weight throughout the winter, and those of first-years increasing from 5.3% in September to reach adult size by mid-January. Data from 1977 and 1978 conform to this pattern, but there was greater variability than in earlier years. In particular three adults in early March had pectoral muscles that formed an exceptionally high percentage ($\bar{x}$ 6.75%) of total lean weight. Since pectoral muscle size in relation to SMV in these birds was similar to other samples (Figure 18a), it follows that this high percentage is a consequence of unusually low total lean weights rather than small pectoral muscles. Low lean weights in these Godwits were due to a significantly lower water content when compared with other adults from 1977 and 1978 (Table 15) since differences in liver weight and total lean dry weight were not involved (Table 15). These values were not affected by sex differences in body size since the sex ratio was the same in both samples (2 females : 1 male).

Body size variation in Bar-tailed Godwits is large, and the degree of sexual dimorphism is amongst the largest that occurs in shorebirds. Seasonal changes in total lean weight could not be examined (see Evans and Smith 1975), but total lean weights from 1977 and 1978 are summarised in Table 16 in comparison with Evans and Smith's values for winter. Within each age-class in 1977 and 1978 females were significantly heavier than males (adults, $t_{19} = 4.17$ $P < .005$; first-years $t_{12} = 4.36$ $P < .002$). In both sexes, adults were heavier than first-years, although the difference was significant only in

Table 15. Water contents, liver weights and total lean dry weights of adult Bar-tailed Godwits in January/February and early March.

	4 March	January/February	Student's t	P
n	3	18		
Water Content (% total lean weight)	65.00 ± 0.40	67.00 ± 0.40	3.50	<.01
Lean Dry Liver (g.)	3.46 ± 0.31	3.68 ± 0.16	0.63	n.s.
Total Lean Dry Wt. (g.)	102.40 ± 9.30	101.00 ± 3.00	0.03	n.s.

Figures are $\bar{x}$ ± 1 s.e.

Table 16. Winter (October - March) total lean weights (g.) of Bar-tailed Godwits at Lindisfarne.

	Adult		First-year	
	Male	Female	Male	Female
1977 - 1978 (this study)	270.8 $\pm$ 8.8 (7)	321.6 $\pm$ 8.4 (14)	256.5 $\pm$ 8.1 (9)	295.8 $\pm$ 3.9 (5)
1970 - 1975 (from Evans & Smith 1975)	272.1 (29)	317.1 (25)	266.0 (33)	313.2 (25)

Values are $\bar{x} \pm 1$ standard error (sample size).

Standard errors could not be calculated for data from Evans & Smith (1975).

females (males, $t_{12} = 1.19$ $P > .10$); females, $t_{17} = 2.78$ $P < .05$). The total lean weights within each age/sex class in 1977 and 1978 were very similar to those during 1970 - 1975 (Table 16).

Curlew, Numenius arquata (L.)

Dates of collection were not recorded for most of the Curlews available since they were shot by wildfowlers. Eleven were collected at Lindisfarne during winter in the early 1970s, and two at Teesmouth on 21 March 1972. Variation in nutritional condition during winter cannot be examined, but condition can be compared with that of other shorebirds. Weights and condition indices of Curlews are summarised in Table 17. Three Curlews from Lindisfarne carried very little fat (lipid indices of 0.1%, 0.7% and 1.4%). Excluding these, the lipid index averaged 7.9% during winter. The highest lipid index was 18.1%.

Pectoral muscle size averaged .279 SMV in the fatter birds in winter; the pectoral muscles formed a small percentage of total lean weight in Curlews ($\bar{x}$ 4.9%) (Table 17). It is not clear whether the three Curlews with virtually no fat in winter also had low protein reserves since no standard muscle volume indices could be calculated for those individuals. However, the correlation between bill-length (as a measure of body size - see Appendix 2 and Townshend 1981a) and total lean dry weight (Figure 19) suggests that these birds did have lower than average lean dry weight for their body size.

Female Curlews were significantly heavier than males (Table 17), in both lean weight ($t_{11} = 6.20$ $P < .001$) and

Table 17. Weights and nutritional condition of Curlews in north-east England in winter.

		n	$\bar{x} \pm 1$ s.e.
Lipid Index (%)		13	6.23 ± 1.36
Pectoral Muscle Index (SMV)		6	.279 ± .004
Pectoral Muscle Index (% LW)		7	4.90 ± 0.10
Lean Weight (g.)	male	5	662.6 ± 11.3
	female	8	867.1 ± 31.0
Lean Dry Weight (g.)	male	5	165.9 ± 6.4
	female	8	217.4 ± 11.7
Lean Dry Liver Weight (g.)	male	3	8.08 ± 0.73
	female	5	8.51 ± 0.57
Water Content (% LW)		10	74.97 ± 0.85

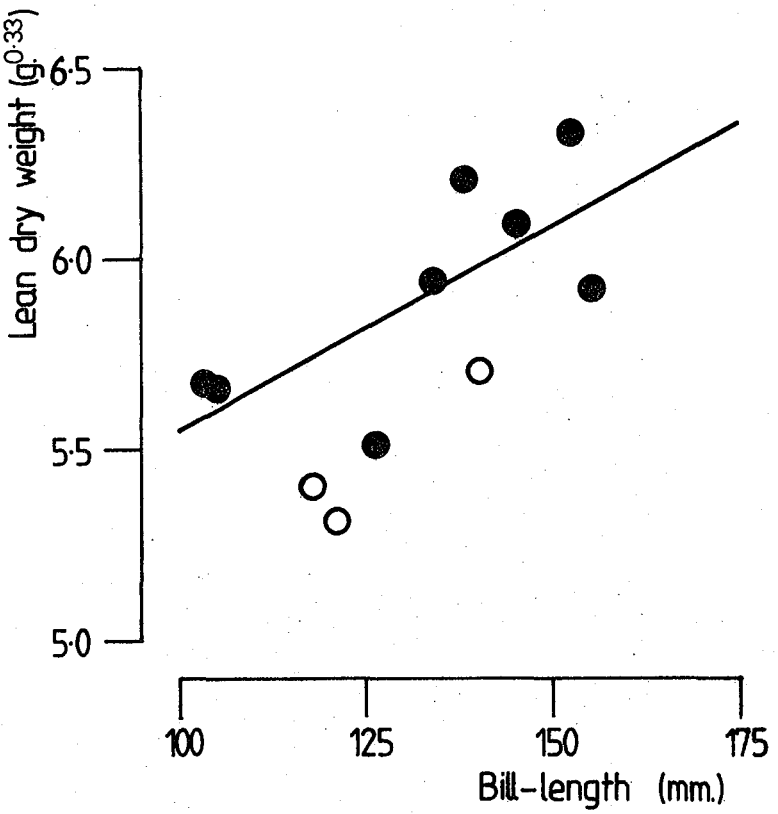

Figure 19: Relationship between the bill-length and lean dry weight of Curlews during winter in north-east England. Points show birds with fat reserves (●) and birds with no fat reserves (o). Regression for birds with fat reserves only is Lean Dry Weight$^{0.33}$ = 0.011 Bill-length + 4.48. r_6 = 0.71 $P < .05$.

lean dry weight ($t_{11} = 3.86$ $P < .01$). In size, Curlews are amongst the most sexually dimorphic of all shorebirds (Prater et al. 1977).

Water content was higher in Curlews ($\bar{x}$ 75% of total lean weight) than in other shorebirds studied.

Turnstone, Arenaria interpres (L.)

The only Turnstones analysed were from Teesmouth on 14 November 1975 (2 first-years, 1 adult) and 23 November 1976 (2 first-years). The nutritional condition of these birds is summarised in Table 18.

Lipid indices of first-year Turnstones in November were low, averaging only 3.6%. These birds may have arrived recently at Teesmouth. Pectoral muscles as a proportion of SMV were small. However, the pectoral muscles formed a large percentage of the total lean weight. Since the water content of first-year Turnstones (67.1 $\pm$ 0.7% total lean weight, n = 4) was very similar to that of other shorebirds, lean dry body components other than the pectoral muscles must contribute a small percentage to total lean weight.

The one adult Turnstone collected in November was in better nutritional condition than the first-year birds, with a lipid index of 12% (Table 18), and slightly larger pectoral muscles. Total body weights of Turnstones on the Wash reach a midwinter peak in January before declining until April (Figure 20). Total body weights at Teesmouth also peak in midwinter. Weights in November and December were very similar at Teesmouth and the Wash, but weights were slightly lower at Teesmouth between January and March.

Table 18. Nutritional condition of Turnstones collected at Teesmouth on 14 November 1975 and 23 November 1976.

	First-year	Adult
n	4	1
Lipid index (%)	3.61 ± 0.39	12.10
Pectoral muscle index (SMV)	0.258 ± 0.016	0.269
Pectoral muscle index (% LW)	6.45 ± 0.32	6.66

Values are mean ± 1 standard error.

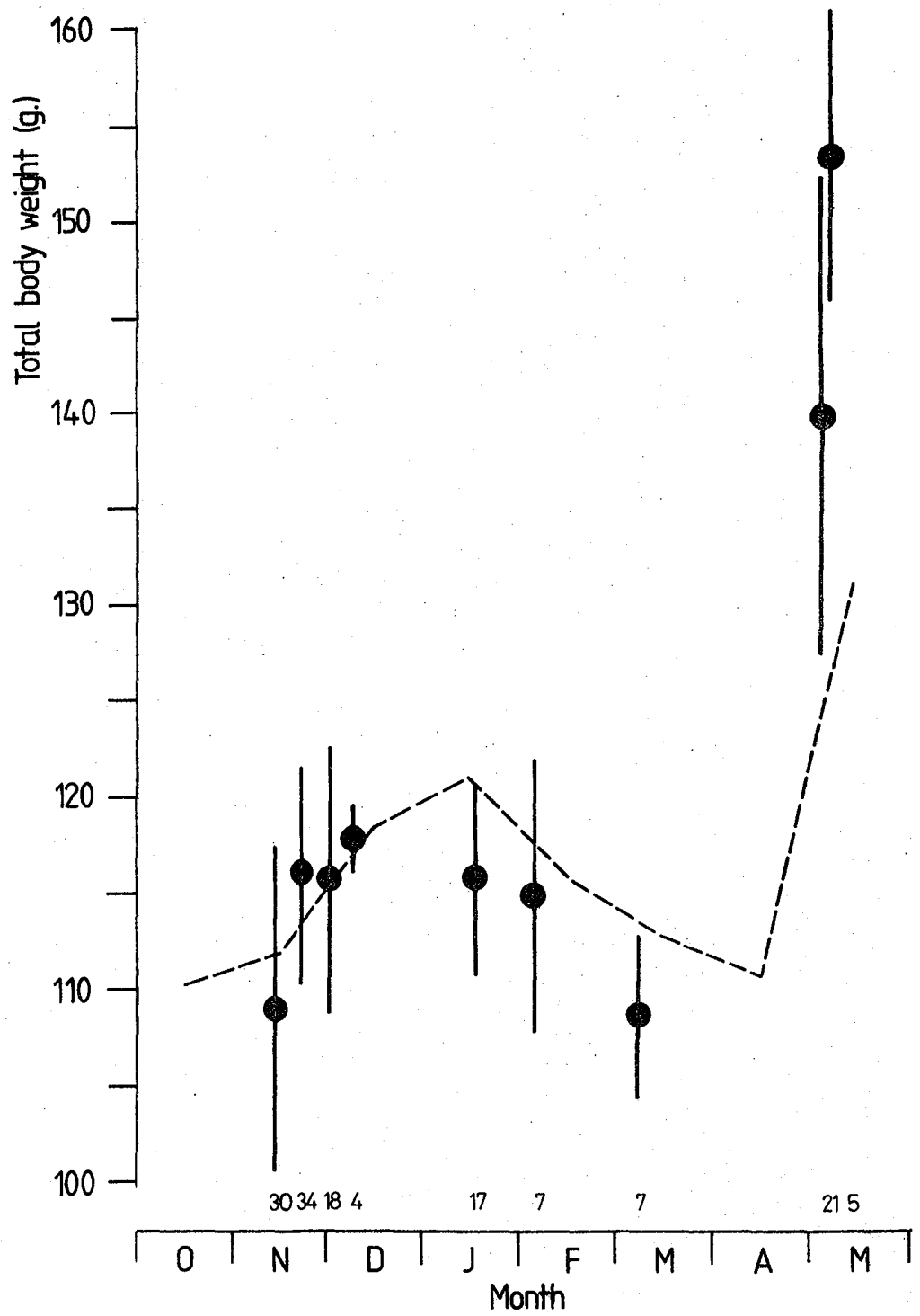

Figure 20: Total body weights of Turnstones at Teesmouth. Points show mean ± 1 standard deviation. Numbers indicate sample sizes. Mean weights from the Wash, from Branson(1979), are also shown (----).

Correlations between the Levels of Fat and Protein Reserves

Evans & Smith (1975) suggested that although fat and protein reserves were independent measures of condition, they frequently, but not always, changed in parallel. If changes occurred in only one reserve, fat (the main energy reserve) rather than protein was most likely to be stored or utilised. Further information is presented below on the relationship between the levels of fat reserves (measured by lipid indices) and protein reserves (measured by pectoral muscle indices) at different times during the non-breeding seasons, in samples that were considered to be in normal condition for the time of year (i.e. not starving). Since patterns of seasonal change are more marked in fat than in protein reserves, samples from different dates and years were examined separately. Correlations are summarised in Table 19.

During autumn and early winter (Table 19a), when fat and sometimes also protein reserves were increasing, correlations were generally positive (i.e. high lipid indices were associated with high pectoral muscle indices). Correlations were significant on some dates in adult Dunlins and Redshanks, and in first-year Dunlins and Knots. Correlations in December may have been masked by the probable recent arrival of most of the Dunlins and Knots sampled at Teesmouth (see later).

In late winter (January - March) the relationships between fat and pectoral muscle size were more variable (Table 19b). Significant positive correlations occurred in adult Dunlins and Golden Plovers in February, but in adult Knots and Bar-tailed Godwits and in all first-year shorebirds correlations were not significant. Lack of correlation would be expected if

Table 19. Correlations between lipid index and pectoral muscle index (SMV) or shorebirds during the non-breeding seasons.

	Date	Adults			First-years		
		n	Spearman r_s	P	n	Spearman r_s	P
a) Autumn/early winter							
Dunlin	14 Sep. 1977	7	.750	<.05			
	12 Oct. 1977	5	.800	n.s.	8	.881	<.01
	9 Dec. 1977	11	.364	n.s.	8	.810	<.05
	16 Dec. 1975	10	.504	n.s.	6	-.257	n.s.
Knot	10 Nov. 1977				6	.943	<.01
	9 Dec. 1977	7	.054	n.s.			
Redshank[1]	18 Nov. 1977	18	.564	<.01			
b) Late winter							
Dunlin	5 Feb. 1977	6	.514	n.s.	7	-.286	n.s.
	12 Feb. 1977	16	.579	<.05	7	-.179	n.s.
	9 Feb. 1978	15	.370	n.s.	11	.155	n.s.
Knot	30 Jan. 1973	14	-.240	n.s.			
	9 Feb. 1978	9	.258	n.s.	6	-.429	n.s.
Bar-tailed Godwit	2 Feb. 1977	10	-.194	n.s.			
	Jan. 1978	5	-.600	n.s.	8	-.226	n.s.
Golden Plover	5/8 Feb. 1978	15	.493	<.05			

Table 19 (cont...)

	Date	n	Spearman r_s	P
c) Spring				
Dunlin[2]	late May	21	.417	$<.05$
Sanderling	April/May	7	.964	$<.01$

Notes: [1] Redshanks were from the Ythan estuary, N.E. Scotland.

[2] Adult and first-year samples combined.

fat reserves had been drawn upon by some birds, but protein had not.

During spring (Table 18c, Figure 21), when lipid indices and pectoral muscle indices were both increasing (Figures 8, 10, 11, 12, 14, 15) there were significant positive correlations in Dunlins and Sanderlings, suggesting that individual birds were simultaneously laying down fat and muscle before migration.

POPULATION TURNOVER AT TEESMOUTH: ITS RELEVANCE TO NUTRITIONAL CONDITION ASSESSED FROM PERIODIC SAMPLES

Shorebird populations show marked changes in size and composition on most estuaries during the non-breeding season. At its simplest, the pattern in one species involves autumn and spring passage, and overwintering populations, often of different racial origins (Fuchs 1973, Pienkowski, Lloyd and Minton 1979, Taylor 1980). The overwintering population on an estuary is not stable and considerable turnover of individuals can occur during the course of a winter (Evans 1980a, Dugan 1981a). Movements and origins of shorebirds using Teesmouth have been discussed by Goodyer and Evans (1980) and details of population turnover at Teesmouth are given by Dugan (1981a) for Knot and Townshend (1981a) for Grey Plover, Curlew and Bar-tailed Godwit. If changes in nutritional condition found between samples taken on different dates are representative of those that would have been made by resident individuals, two criteria need to be satisfied: 1) a resident overwintering population must be demonstrated, and 2) changes in the nutritional condition of individuals in this resident overwintering population must follow the same pattern as that derived from periodic samples.

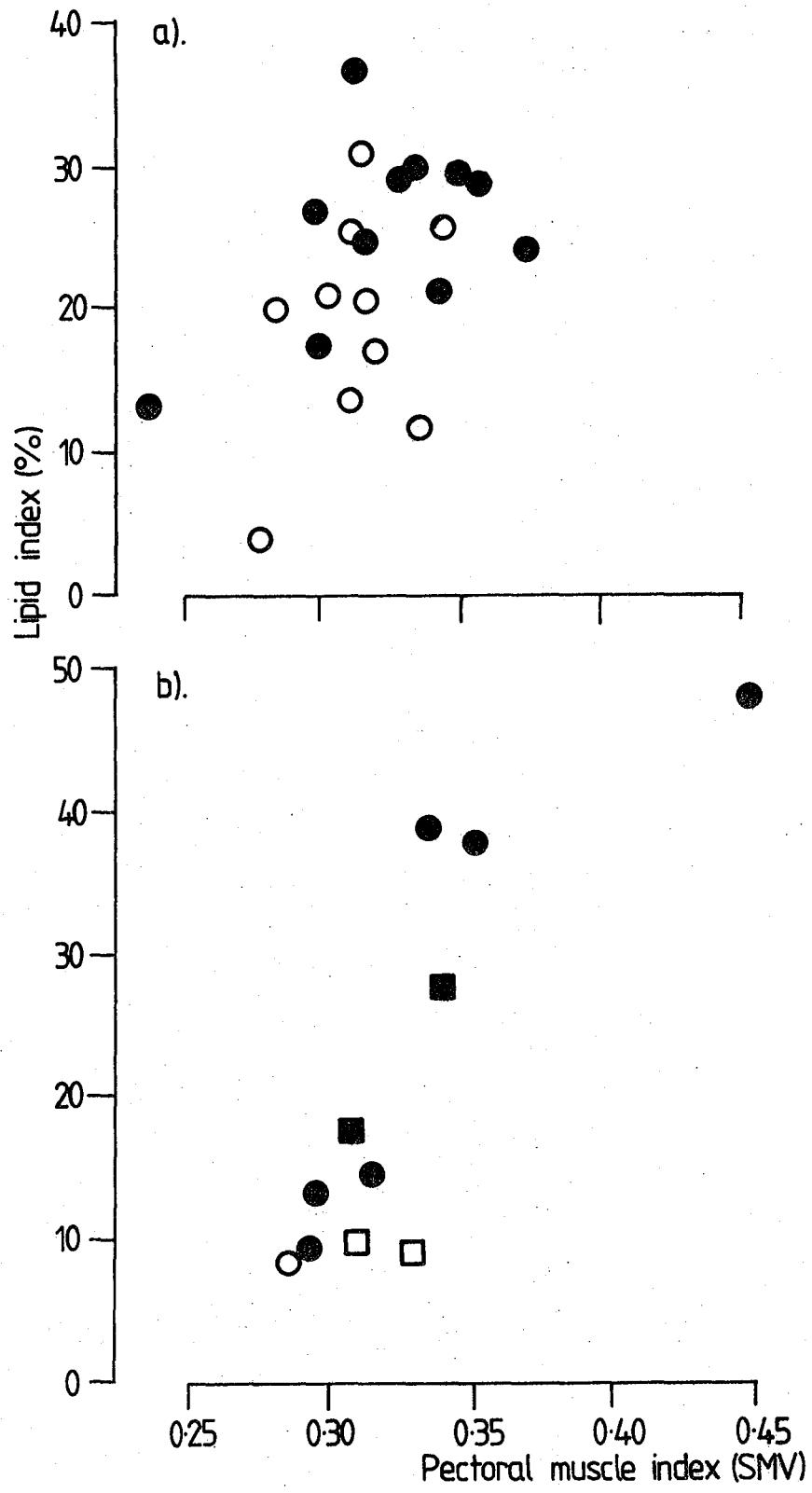

Figure 21: Pectoral muscle size and lipid index of shorebirds during pre-migratory fattening in spring at Teesmouth.
a) in adult (●) and first-year (○) Dunlins during May;
b) in adult Sanderlings during April (○) and May (●) and adult Ringed Plovers during April (□) and May (■).

This section documents population changes at Teesmouth, and movements to and from other estuaries only where these are important for the interpretation of seasonal changes in nutritional condition, using information from population counts and ringing recoveries. It is not intended as a comprehensive demographic study. Changes in the condition of individuals are examined using within-winter changes in total body weight. Finally the effect of population turnover on the observed levels of nutritional condition of Dunlins and Knots in early December is examined.

Seasonal Changes in Shorebird Populations

Dunlin

Calidris a. alpina (breeding in Northern Scandinavia and Russia) is the only race of Dunlin overwintering at Teesmouth, and only this race was represented in nutritional condition samples. (*C. a. schinzii* (breeding around the Baltic, Western Europe and Iceland) is present only on spring and autumn passage.) In most winters the number of Dunlins increases between October and December or January, with a peak of between 3,500 and 5,000 in recent years (Figure 22). After mid-winter the population declines until March, when spring passage birds begin to arrive, many of these being *schinzii* (Goodyer and Evans 1980). It is not known to which estuaries *alpina* Dunlins move when they leave Teesmouth in late winter.

Despite the large seasonal changes in the population, some individual Dunlins remain at Teesmouth throughout the winter (Figure 23). Many Dunlins arriving in November/December remained until the end of February. Additionally, Dunlins caught in September have been recaptured in most later months in the same winter. Some overwintering Dunlins also occurred

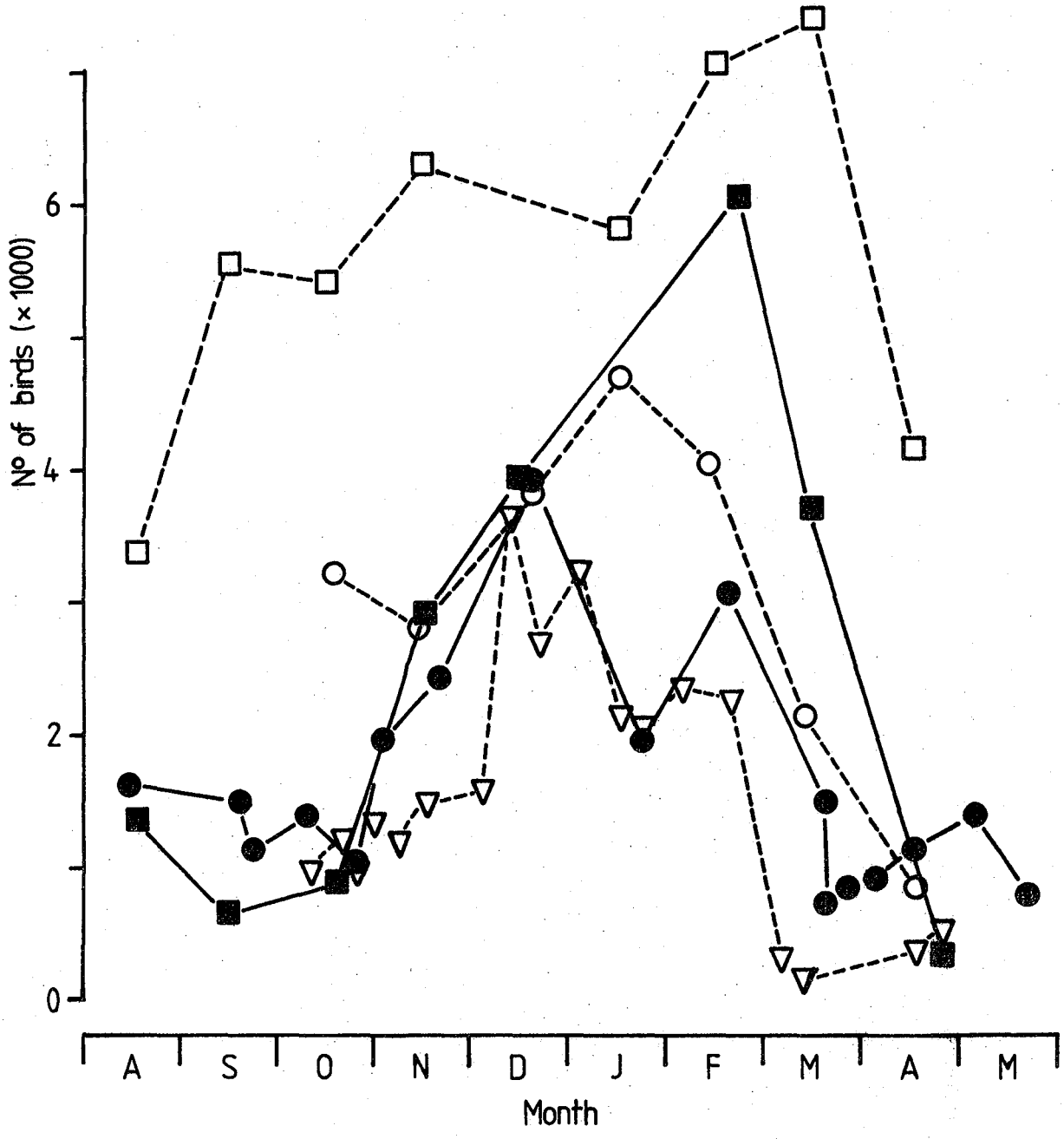

Figure 22: Population size of Dunlins at Teesmouth during the non-breeding seasons. Symbols as Figure 11. Counts for 1978/79 from Davidson (1980); all others from L. R. Goodyer and Birds of Estuaries counts made by Teesmouth Bird Club.

at Teesmouth in May, although these birds had probably moved away from Teesmouth in late winter, before returning on spring passage (Goodyer and Evans 1980). There is evidently a strong resident component in the Dunlins wintering at Teesmouth, and resident individuals can be demonstrated in most of the catches in each winter from which nutritional condition samples were collected (Figure 23). Part of the wintering population is known to return to Teesmouth in subsequent years: one adult has been caught in both December and February in four different years and, in catches from which condition samples were taken, one adult was caught on both 16 December 1975 and 12 February 1977, and two adults were caught on both 12 February 1977 and 9 December 1977. Information on the weight changes of individual Dunlins at Teesmouth is scant. Average individual weight changes (Table 20) do conform to the fat reserve pattern (Figures 11 and 12) of a peak in midwinter followed by a decline.

Knot

Knot populations at Teesmouth, like Dunlins, reached peak numbers in midwinter (Figure 24). Few Knots arrived at Teesmouth before November, after which the population rapidly increases, most usually arriving by mid-November; but in the 1977/78 winter the main arrival was between mid-November and mid-December. Most Knots left Teesmouth between late February and March.

After their arrival in November/December, some Knots remain at Teesmouth for the rest of the winter, but fewer Knots than Dunlins have been caught twice in the same non-breeding season (Figure 25, Table 21), although this was

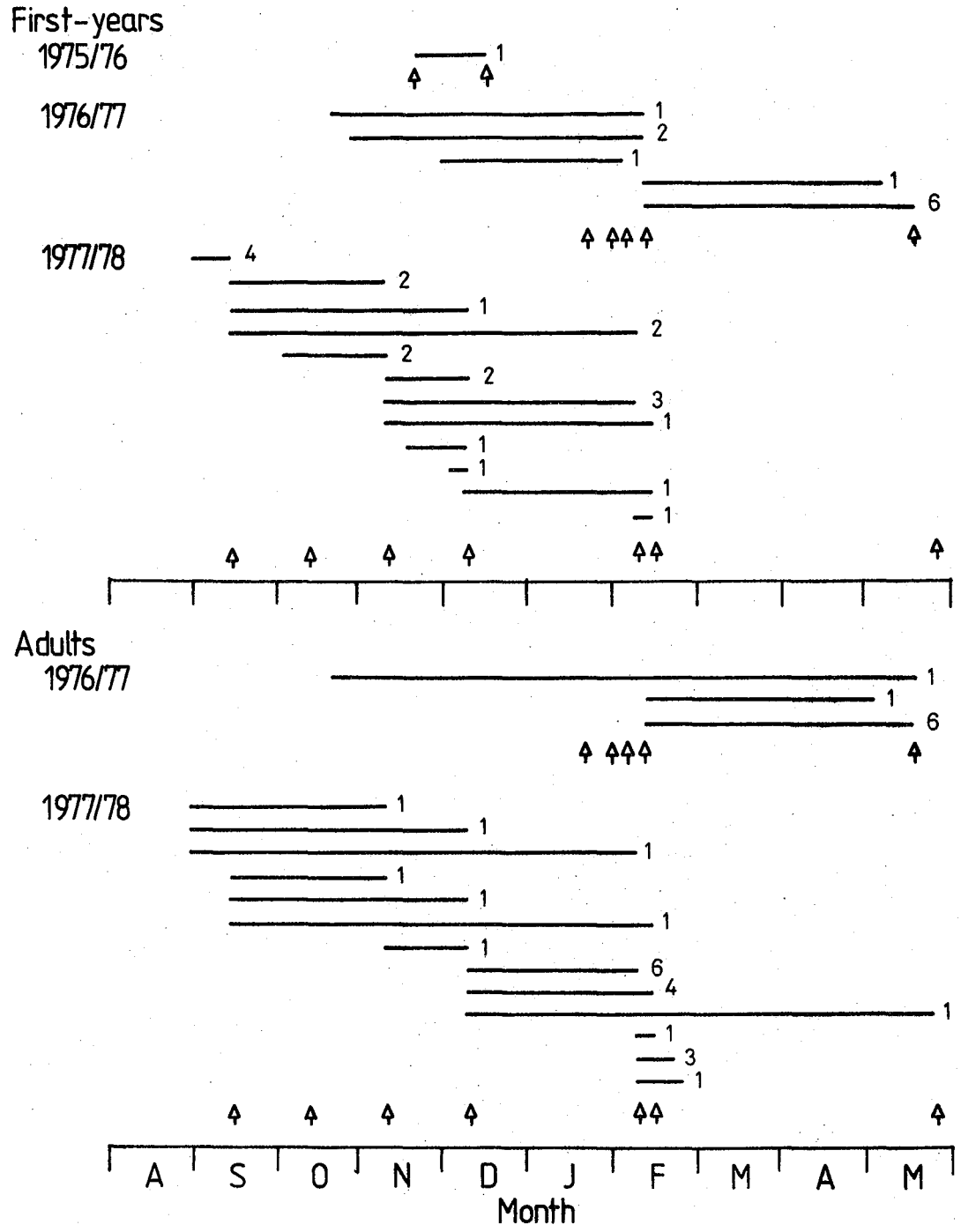

Figure 23: Records of Dunlins caught twice during the same non-breeding season at Teesmouth up to May 1978. Horizontal bars join dates of first and second capture and numbers indicate number of individuals. Arrows indicate catches from which nutritional condition samples were collected.

Table 20. Mean changes in the total body weight of Dunlins caught twice within one year at Teesmouth, grouped for early and late winter.

	Adults		First-years	
	n	mean change (g.)	n	mean change (g.)
October - December			5	+3.5
January - February*	4	-3.8	2	-4.0

* Individuals weighed during severe weather in January/ February 1979 are excluded.

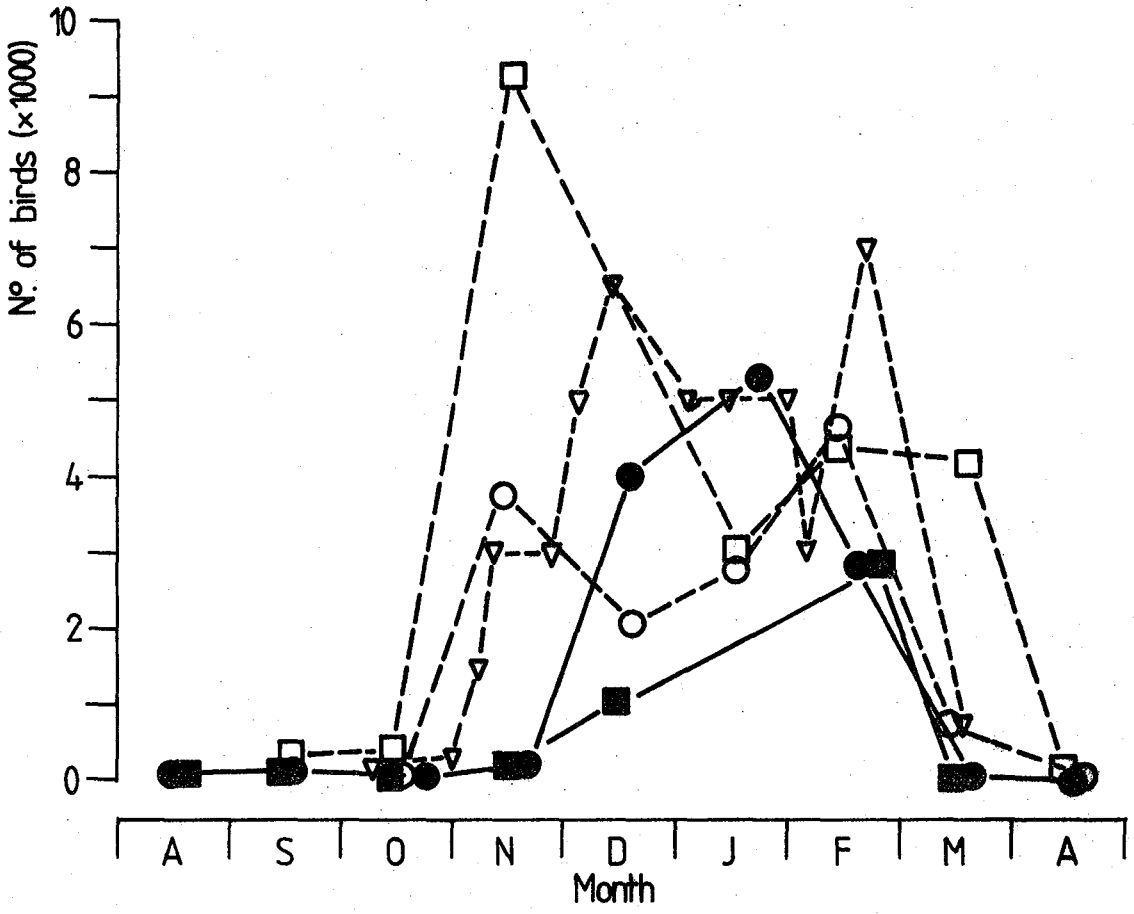

Figure 24: Population size of Knots at Teesmouth during the non-breeding seasons. Year symbols as Figure 11. Counts for 1978/79 from Davidson (1980); all others from P. J. Dugan, L. R. Goodyer and Birds of Estuaries Counts made by Teesmouth Bird Club.

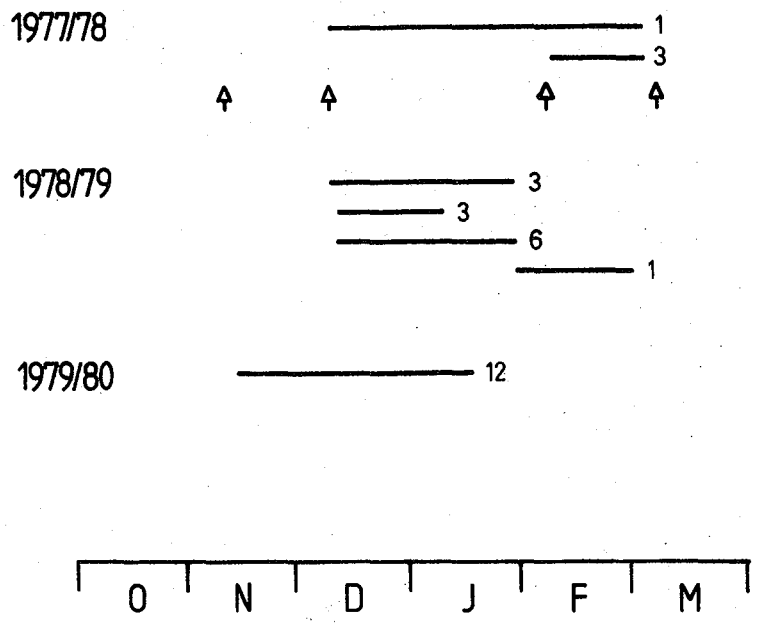

Figure 25: Records of adult Knots caught twice during the same non-breeding season at Teesmouth. Horizontal bars join dates of first and second capture and numbers indicate number of birds. Arrows indicate catches from which nutritional condition samples were collected.

Table 21. Numbers of Dunlins and Knots caught at Teesmouth twice during one non-breeding season.

	No. of catches	No. of Individuals		% caught twice
		caught once[1]	caught twice	
Dunlin				
1975/76	2	78	1	(1.28)
1976/77	7	537	19	3.54
1977/78	11	1,015	44	4.33
Knot				
1976/77	4	160	0	(0)
1977/78	2	562	4	0.71
1978/79	9	1,225	16[2]	1.31
1979/80	5	943	12	1.27

[1] excluding birds caught for the first time in May, since these have little chance of being recaptured before departure for breeding grounds.

[2] includes 3 first-year birds not shown on Figure 25.

partly because fewer catches of Knot were made within each winter (Table 21).

However, after their arrival at Teesmouth in November/ December, some Knots are known to move to other estuaries within the same winter (Goodyer and Evans 1980, Dugan 1981a). Most records refer to birds moving to other estuaries in Britain, generally further north, but one bird had moved south to the Humber by the end of December, and another, caught at Teesmouth in mid-November had moved to Denmark by 1 January in the same winter. Movements of ringed Knots away from Teesmouth occurred in the period mid-November (i.e. soon after the arrival of most Knots) to late January.

Dye-marking studies in 1979/80 showed turnover and rapid onward movement of Knots from Teesmouth in November and December (Dugan 1981a). 20% of Knots marked in mid-November left Teesmouth within one month, and northwards passage through the Tees also occurred in 1978/79. Dugan (1981a) concluded that many Knots wintering on east coast estuaries moved between several estuaries during one winter.

The evidence of population turnover, coupled with the low numbers of Knots caught twice during the same winter, mean that observed seasonal changes in nutritional condition could result from the sampling of different populations rather than changes in the condition of individuals. However individual adult and first-year resident Knots lost weight after midwinter (Figure 26), thus conforming to the pattern of fat reserves described from periodic samples (Figure 5). Only one Knot has been weighed twice before midwinter: a

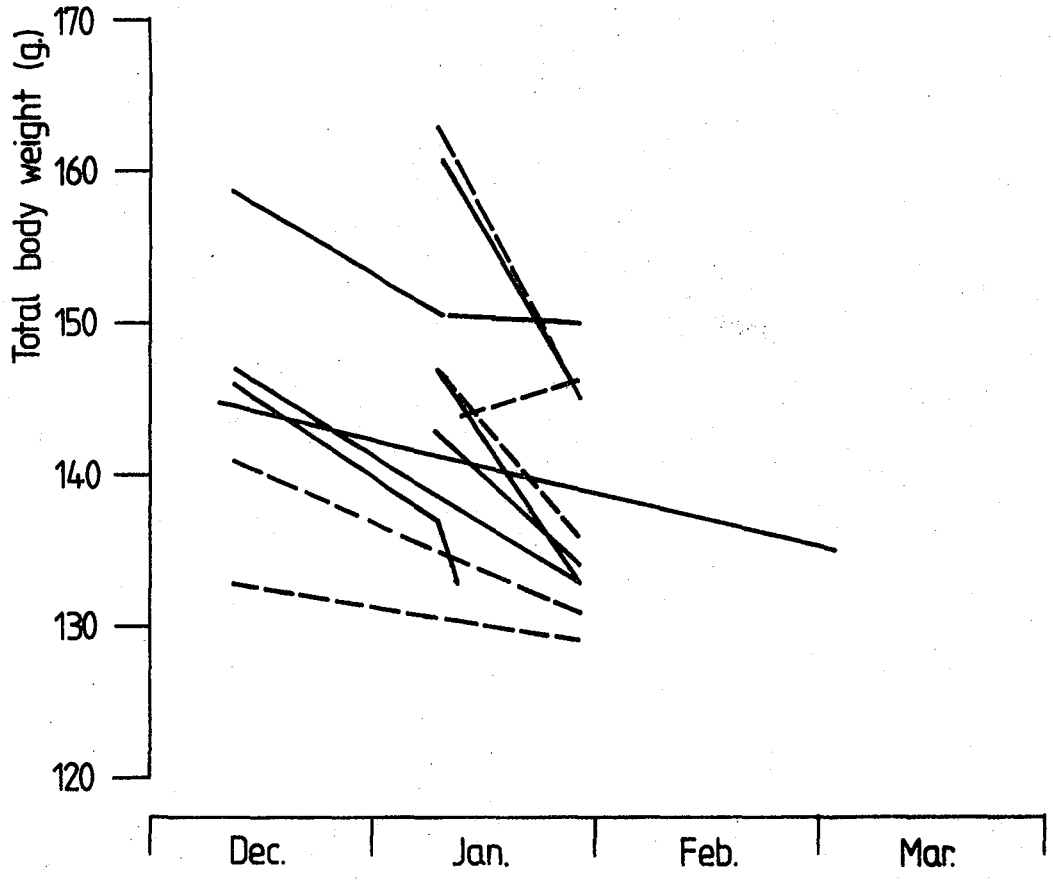

Figure 26: Within-year weight changes of adult (——) and first-year (----) Knots at Teesmouth during winter. Each line joins the weights of one individual.

first-year bird which gained weight during November.

Sanderling

At least three populations of Sanderling use Teesmouth during the non-breeding season: an autumn moulting flock, augmented by late autumn arrivals to form a wintering population, and an additional spring passage population (Goodyer and Evans 1980). The wintering population is complex (Evans, Brearey and Goodyer 1980), with some Sanderlings remaining close to Teesmouth all winter, but others apparently being more mobile and occurring at Teesmouth only sporadically throughout the winter. Many of the wintering population remain at Teesmouth until late May (Brearey 1981). Individual resident Sanderlings gain weight before midwinter and lose weight thereafter (Figure 27), the typical seasonal pattern of shorebird fat reserves at Teesmouth.

Grey Plover

Dugan (1981a) and Townshend (1981a) found that many individually-marked Grey Plovers were resident throughout the winter, with few departing before March. The estimates of lipid indices at Teesmouth (Figure 4) were made on these marked birds. Those winter residents that have been weighed twice within one winter (Figure 28) show a midwinter peak in total body weight and weight loss after midwinter.

Other Species

There are no relevant within-winter weight changes of Curlews, Bar-tailed Godwits, Ringed Plovers or Turnstones. Many Curlews and Bar-tailed Godwits (Townshend 1981a) and most Turnstones (Brearey 1981) are winter residents at Teesmouth.

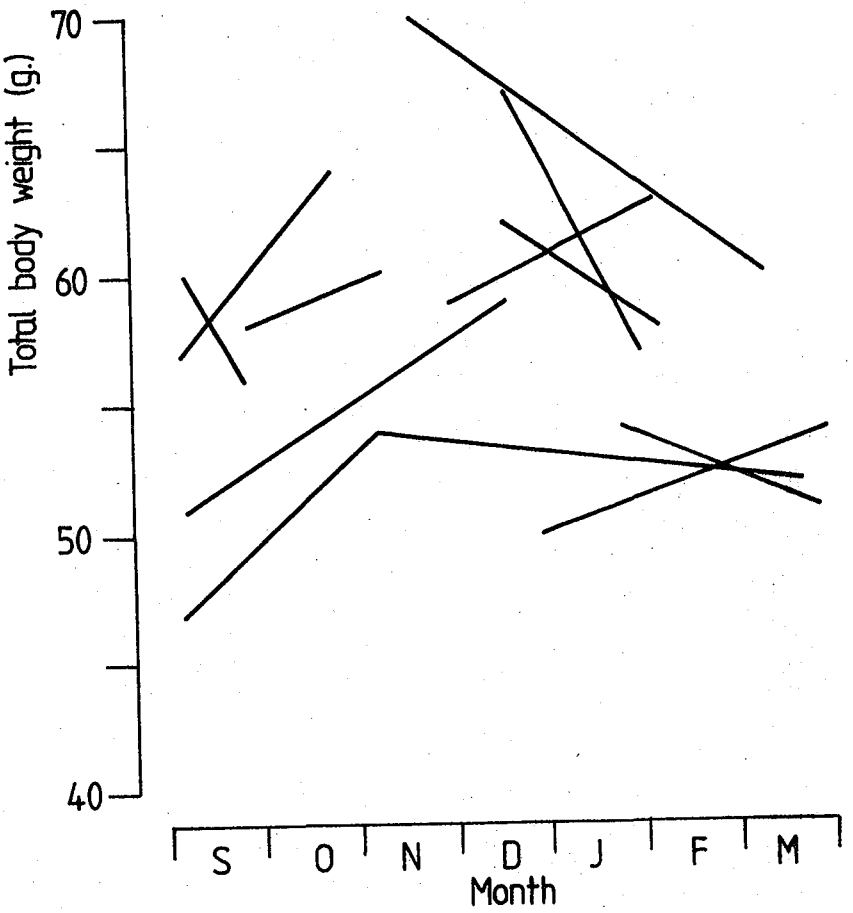

Figure 27. Within-year weight changes of adult Sanderlings at Teesmouth. Each line joins the weights of one individual. Only birds weighed twice during early or late winter are shown.

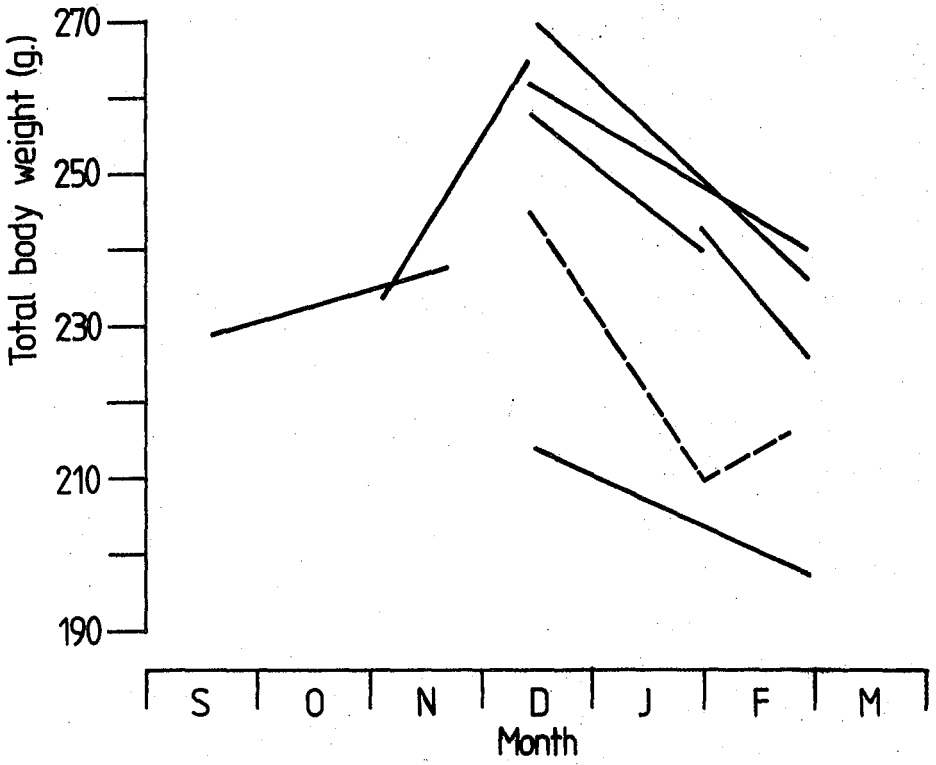

Figure 28: Within-year weight changes of adult (——) and first-year (----) Grey Plovers at Teesmouth. Each line joins the weights of one individual.

There is no information on the population turnover of Ringed Plovers.

Nutritional Condition of Dunlins and Knots Samples in early December

Dunlins collected on 16 December 1975 and 9 December 1977, and Knots collected on 9 December 1977 (even after correction for condition loss in captivity (Appendix 1)) had markedly lower average lipid indices than the expected values of at least 15% fat for resident birds (see Results). In Dunlins, averages were only 11.6% (n = 10) in adults and 9.8% (n = 6) in first-years in 1975, and were 8.5% (n = 11) and 8.9% (n = 8) respectively in 1977. Knot in December 1977 had average lipid indices of 8.5% (adults n = 7) and 13.1% (first-years n = 3). The poor fat condition of most birds in those samples could be due to either the catabolism of some fat reserves during a preceding period of severe weather, or to emigration of parts of the populations with above average lipid indices, or the arrival at Teesmouth of birds with low lipid indices.

Weather conditions during the week before the collection of samples were unlikely to have induced the use of fat reserves. In early December 1977 both air and mud temperatures remained well above $0^{\circ}C$, and there was only one day of strong winds that would have greatly increased the energy requirements for thermoregulation or impaired feeding (see Paper 2).

There is no evidence either from changes in population size or from ringing recoveries of large-scale emigration by either Knots or Dunlins in early December. Thus the most likely explanation is the arrival at Teesmouth, a few days before sampling, of Dunlins and Knots with low lipid indices. Evidence supporting this interpretation is given below.

Population Size

Between mid-November and mid-December the Dunlin population at Teesmouth (Figure 22) increased by 25.5% in 1975 and 38.5% in 1977. The main arrivals of Knot also occurred between mid-November and mid-December (Figure 24), the population at Teesmouth increasing from 200 to 4,000 birds during this period in 1977. Counts at only monthly intervals were available for those years, but more frequent counts in 1978/79 show a main arrival period between 4 - 12 December. Assuming a similarly timed arrival in previous years, recently-arrived Dunlins would have been at Teesmouth for maxima of five days in 1977 and 12 days in 1975 before samples were collected. The timing of the main Knot arrival is more variable.

Liver Weights

Lean dry livers of Dunlins on 9 December 1977 were significantly lighter than those of the later December sample from 1975, and that of a sample in February 1977 that had probably wintered at Teesmouth for several months (Table 22). A similar pattern, of low liver weight on 9 December 1977, emerges from small samples of Knots (Table 22). These low liver weights are consistent with recent immigration, since most losses of lean dry liver weight were probably glycogen

Table 22. Weight (g.) of the lean dry liver and liver fat of Dunlins and Knots in December and February.

	December		February	
	Date	$\bar{x} \pm 1$ s.e.(n)	Date	$\bar{x} \pm 1$ s.e.(n)
a) Lean Dry Liver				
Dunlin				
1975/76	16th	.985 ± .026 (16)*		
1976/77			5th	.889 ± .028 (15)
			12th	.990 ± .027 (23)**
1977/78	9th	.848 ± .043 (5)	9th	.867 ± .027 (14)
Knot				
1976/77			5th	3.067 ± .294 (3)
			12th	2.080 ± .040 (2)
1977/78	9th	2.410 ± .060 (2)	9th	2.868 ± .095 (4)
b) Liver Fat				
Dunlin				
1975/76	16th	.098 ± .006 (16)**		
1976/77			5th	.095 ± .007 (15)*
			12th	.080 ± .005 (23)
1977/78	9th	.070 ± .007 (5)	9th	.066 ± .004 (14)

Significantly different weights from 9 December 1977 are * $P < .05$, ** $P < .02$ (Student's t-tests).

losses, known to occur during migration in other birds (King, Barker and Farner 1963). Weights of liver fat followed a similar pattern to lean dry liver weight. In Dunlins, weights of liver fat were significantly lower on 9 December 1977 than on either 16 December 1975 or 5 February 1977 (Table 22), suggesting possible differences in metabolic state on 9 December 1977.

Other Lean Body Components

Total lean weights of Dunlins were higher on 9 December 1977 and 16 December 1975 than in the preceding month of each year (Figure 16). The differences were in lean dry components since water content was unchanged between November and December in each year. The components responsible for the differences are not known, but pectoral muscle size was not involved as this remained unchanged (Figure 14). The pectoral muscle size of adult Knots was lower in December 1977 than in other samples from that winter (Figure 6), consistent with the loss of pectoral muscle tissue during a flight to Teesmouth (Evans 1969b, Pennycuick 1978). No differences in total lean weights were detected, but samples were very small.

The Sources of Dunlins and Knots arriving at Teesmouth in early December

The estuaries used by Dunlins and Knots immediately before their move to Teesmouth cannot be firmly identified. Ringing evidence indicates that some adult Dunlins that had moulted on the Wash, and were ringed in August and September, had moved the 220 km. north to Teesmouth later in the same winter. Unfortunately there are no records of these birds being on the Wash, or elsewhere, after September and none have been caught at Teesmouth before 11 December. These birds either

remained undetected on the Wash or moved to other estuaries, e.g. the Humber, before moving to Teesmouth in December. The early December arrivals may sometimes include Dunlins from elsewhere than the Wash, as indicated by an adult ringed at Tentsmuir (Fife), 200 km. north, on 1 November 1975 and caught at Teesmouth on 16 December 1975. Other adult Dunlins wintering at Teesmouth are known to have moulted in autumn on the Dutch and German Waddenzee (Goodyer and Evans 1980), but little is known of the early winter movements of first-year Dunlins that winter at Teesmouth.

Many Knots arriving at Teesmouth in November/December have probably come from the Wash. Eighteen adults ringed there between August and mid-November have been caught in later winters at Teesmouth (Goodyer and Evans 1980). Additionally, two within-year movements from the Wash to Teesmouth are known: one adult ringed on the Wash in August 1977 and caught at Teesmouth on 9 February 1978, and one adult marked with coloured dye on the Wash in October 1979 and seen at Teesmouth in November, one month later (Dugan 1981a). No Knots caught elsewhere than on the Wash in autumn have been recorded at Teesmouth in the same winter.

The nutritional condition of a bird on its arrival at Teesmouth is primarily a product of the nutritional condition before departure from another estuary, and the weight of fat, protein and water lost during the flight from that estuary. If these measures were known, expected lipid indices of birds arriving at Teesmouth from various estuaries could be calculated. Table 23 gives the methods of calculation. The expected lipid indices are subject to several errors which cannot be corrected,

Table 23. Calculation of the expected lipid index (fat (g.) as a percentage of total body weight (g.)) of a shorebird arriving at Teesmouth from another estuary.

1. Calculate estimated fat (g.) and lipid index on source estuary.	Fat (g.)	=	total body wt. - lean wt.[1]
	Lipid Index (%)	=	$\frac{\text{fat}}{\text{total body wt.}} \times 100$
2. Calculate fat (g.) used during flight from source estuary to Teesmouth.[2]	Fat used on flight (g.)	=	$\frac{\text{distance flown (mls) x flight metabolism}}{\text{flight speed x 9.1 Kcals}}$
3. Calculate expected lipid index on arrival at Teesmouth.[3]	Expected Lipid Index (%)	=	$\frac{\text{fat on source estuary - fat used on flight}}{\text{total body wt. on source estuary - fat used on flight}} \times 100$

1 Average lean weights from Appendix 2.

2 Formula derived from McNeil & Cadieux (1972).

3 Assuming minimal losses of muscle and water (see Tucker 1968, Pennycuick 1969) during flight.

particularly the assumptions that departing birds have the same lipid indices as those that remain, that no lean body components are used during the flight, and that the formulae in McNeil and Cadieux (1972b) are reasonable estimators of flight metabolism and flight range. Given these constraints, some conclusions can be made.

The expected lipid indices of adult Dunlins and Knots on arrival at Teesmouth, compared with the values in the samples from 9 December 1977 (Table 24) again indicate the Wash as the most likely source of both Dunlins and Knots. First-year birds of both species from the Wash conform to this interpretation (Table 24), but weights were not available from other estuaries. If adult Dunlins and Knots had moved to Teesmouth from other estuaries, then to arrive with the observed lipid indices, these birds would have carried below-average lipid indices on departure from their source estuary. This seems unlikely since some fat is required for the flight. Both Dunlins and Knots might also have moved directly to Teesmouth from the Waddensee. Few Dunlins or Knots have been weighed on the Waddenzee in December (Smit and Wolff 1981) but by making the reverse of the calculations in Table 23 it can be predicted that to arrive in the observed condition total body weights at departure should average 58.5 g. and 57.5 g. in adult and first-year Dunlins, and 161 g. in adult Knots. These weights correspond to lipid indices of 14.3%, 14.9% and 15.3% respectively. Involvement of birds from the Waddensee must wait for future confirmation.

Dunlins and Knots arriving at Teesmouth in early December should deposit fat rapidly, and so have low lipid

Table 24. Expected lipid indices (fat as % of total body weight) of Dunlins and Knots arriving at Teesmouth in early December. (See Table 23 for methods of calculation).

	Expected Lipid Index (%)				Observed Lipid Index (%) at Teesmouth on 9 December 1977
	Wash	Humber (Spurn)	Forth	Morecambe Bay	
Dunlin[1]					
Adult	8.3	12.5	13.3	11.0	8.5
First-year	9.5				8.9
Knot					
Adult	7.4[2]			10.4[3]	8.5
First-year	5.8[2]				

1 total body weights of Dunlins from Pienkowski, Lloyd & Minton (1979).

2 total body weights from Branson (1979).

3 total body weights from Prater (1975).

indices for only a few days after their arrival, otherwise their chances of survival would be less than those of the 'resident' populations should severe weather occur soon after the early December influx. However, low lipid indices in these birds cannot be regarded as deviations from the normal seasonal pattern of fat levels (i.e. that shown by resident individuals throughout the winter). Since the influx of Dunlins and Knots in November and December is a regular phenomenon (Figures 22 and 24), depressed lipid indices in these populations must occur temporarily every year. Similar loss of condition in both fat and protein reserves, as a consequence of migration is known to occur in autumn in Dunlins (Figures 11 and 14) and Bar-tailed Godwits (Evans & Smith 1975) in north-east England. Low total lean weights in autumn, as a result of migratory losses, occur widely in shorebirds and other birds (Paper 3).

DISCUSSION

Functions of Nutritional Reserves during Migration and Moult Periods

Fat Reserves

It is well known that fat is the main fuel for migratory flights in shorebirds (e.g. Johnston & McFarlane 1967, Page & Middleton 1972, McNeil & Cadieux 1972a) as well as in other orders of birds (King 1972, Blem 1976). Migrant shorebirds occur in north-east England in both autumn when non-moulting birds use Teesmouth as a migration stop-over for fat deposition before further movement to wintering grounds, and in spring when both passage birds (on migration stop-over) and winter residents deposit fat before departure to breeding grounds (Evans 1966, Goodyer & Evans 1980).

Lipid indices of shorebirds at Teesmouth compare well with values recorded for other areas and species in both autumn (Table 25) and spring (Table 26). However, comparative information on the same species in different areas is scant. First-year Dunlins caught at Teesmouth in mid-September carried less fat than in Southern Sweden or the Dutch Waddensee at the same time of year (Table 25). However, the birds at Teesmouth, and possibly some of the Southern Swedish samples may have carried rather low fat reserves if they had recently arrived at the stop-over and had not deposited all the fat needed for the next stage of migration. Some autumn passage Dunlins at Teesmouth had a steady weight before depositing fat for further migration (Figure 13). Incomplete fat storage may also apply to other samples taken at migration times.

In spring mean peak fat reserves were generally higher than in autumn (Table 26), as were maximum levels. Large fat reserves are deposited before spring departures from many wintering areas, e.g. northern temperate (such as Teesmouth), equatorial (such as Venezuela) and southern temperate (such as South Africa). As might be expected, there are differences in the timing of spring fattening that relate to differences in the timing of departures, dependent upon the distance between the wintering and breeding grounds. On southern temperate and equatorial wintering grounds most shorebirds began fattening in February or early March, and most have left on northwards migration by late April or early May (McNeil 1970, Thomas & Dartnall 1970, Summers & Waltner 1979). At Teesmouth, adult Dunlins started fattening in early March, first-year Dunlins in late March and Sanderlings in April. Maximum fat loads are

Table 25. Lipid indices of migrant shorebirds in autumn

	Area	Mean peak lipid index (%)	Individual Peak lipid index (%)	Source
a) Fat as % total body weight				
Calidris alpina (1st yr.)	S. Sweden	12	29	Mascher & Marcstrom (1976)
		15	29	" " "
" "	Teesmouth	9	12	This study
C. alpina (adult)	Waddensee	-	29	Smit (1981)
C. pusilla	Ontario	18	42	Page & Middleton (1972)
C. mauri	Alaska	-	18	Johnston (1964)
Charadrius hiaticula	Teesmouth	-	29	This study
Pluvialis squatarola	"	-	35	" "
P. dominica	Alaska	-	12	Johnston (1964)
b) Fat as % lean dry weight[a]				
Calidris alpina (1st yr.)	S. Sweden	57	140	Mascher & Marcstrom (1976)
		59	125	" " "
" "	Teesmouth	33	45	This study
C. fuscicollis	Gulf of St.Lawrence, Canada	175[b]	-	McNeil & Cadieux (1972a)
C. minutilla	"	225[b]	-	" "
C. pusilla	"	175[b]	-	" "
C. canutus	"	225[b]	-	" "
Tringa melanoleuca	"	50[b]	-	" "
T. flavipes	"	125[b]	-	" "
Limnodromus griseus	"	175[b]	-	" "
Limosa haemastica	"	125[b]	-	" "
Charadrius hiaticula	Teesmouth	-	126	This study
Pluvialis squatarola	"	-	152	" "

[a] This measure is included because values from McNeil & Cadieux (1972a) could not be calculated as fat as a % of total body weight.

[b] Values rounded to nearest 25%.

Table 26. Premigratory lipid indices of shorebirds in spring

	Area	Mean peak lipid index (%)	Individual peak lipid index (%)	Source
Calidris alpina	Waddensee	16	25	Smit (1981)
C. alpina	Teesmouth	32	37	This study
C. alba	"	27	47	" "
Charadrius hiaticula	"	22	27	" "
Calidris ferruginea	South Africa[a]	34	-	Summers & Waltner (1979)
C. canutus	" "	34	-	" "
C. minuta	" "	35	-	" "
C. alba	" "	42	51	" "
Tringa terek	" "	34	-	" "
Arenaria interpres	" "	40	41	" "
Pluvialis squatarola	" "	38	-	" "
Calidris fuscicollis	Venezuela	18	20	McNeil (1968)
C. minutilla	"	22	27	"
C. pusilla	"	25	26	"
Tringa flavipes	"	14	22	"
Actitis macularia	"	21	25	"
Catatrophorus semipalmatus	"	32	42	"
Charadrius semipalmatus	"	23	30	"
Pluvialis squatarola	"	14	30	"
Pluvialis dominica fulva	Wake Is., Pacific Ocean	-	44	Johnston & McFarlane (1967)

[a] Values from Summers & Waltner (1979) are overestimates because spring increases in lean weight were not taken into account.

achieved in late May. Similar timings of total body weight gain (much of which is fat - see Table 4) occur in Ringed Plovers, Grey Plovers, Turnstones, Knots, Dunlins and Sanderlings on the Wash (Branson 1979). These differences in timing mean that individuals of the same species wintering at different latitudes probably arrive on arctic breeding grounds at about the same time of year. There is some evidence for this in Knots (Dick 1979).

Highest rates of fattening (assessed by total body weight gain) were recorded in autumn (Table 27). However, all recorded fattening rates are underestimates, those based on recaptured individuals because of stress induced weight loss lasting several days after capture (Appendix 1), and those based on average population weight gains because very fat birds may leave before lean birds (Page & Middleton 1972). There is also some evidence that fattening becomes increasingly rapid during spring (see Figures 11 and 12; and Pienkowski, Lloyd & Minton 1979). Therefore maximum rates of fattening may be similar in autumn and spring.

The high rates of fat deposition in both autumn and spring indicate that at these seasons food intakes of migrants are much greater than are needed to balance energy requirements. High food intake is facilitated by high temperatures causing increased prey availability (Goss-Custard 1969, Smith 1975, Goss-Custard et al. 1977a, Evans 1979, Pienkowski 1980a, b) and low energy requirements for thermoregulation. Prey density, however, is likely to be lower in spring than autumn since in most years it will not have increased by the time spring fattening occurs (see e.g. Gray 1976, Goss-Custard et al. 1977a), though the availability of large prey may be higher.

Table 27. Total body weight gains by migrant shorebirds

Species	Area	Average wt. gain		Source
		g day^{-1}	% total lean wt. day^{-1}	
a) Autumn				
Calidris alpina (1st yr.)	Teesmouth	1.0	2.3	This study
C. ferruginea	Mauritania	0.3	0.5	Wilson, Czajkowski & Pienkowski (1980)
C. ferruginea	Wash	3.9	7.0	Stanley & Minton (1972)
C. pusilla	Ontario	1.3	5.0	Page & Middleton (1972)
b) Spring				
C. alpina (1st yr.)	Wash	1.2	2.0	Pienkowski, Lloyd & Minton (1979)
C. ferruginea	S. Africa	0.7[a]	1.3	Elliott *et al.* (1976)
C. canutus	Morecambe Bay	1.7[a]	1.3	Prater & Wilson (1972)
C. canutus	Iceland	3.0[a]	2.0	" "
C. canutus	S. Africa	1.5[a]	1.2	Summers & Waltner (1979)
C. alba	"	0.8[a]	1.6	" "
Arenaria interpres	"	1.1[a]	1.1	" "
A. interpres	Iceland	3.3[a]	3.0	Morrison & Wilson (1972)
Charadrius hiaticula	Morecambe Bay	2.0	3.5	Clapham (1978)

[a] Calculated from average population weight gain, others from weight gains of individuals.

Many shorebirds probably depart on long-distance migrations with fat levels (Table 26) at or near the maximum recorded level of 45-50% of total body weight found in passerine migrants (Odum 1965). Fat reserves of this size are close to the theoretical maximum that shorebirds are able to carry (Pennycuick 1975). The fat reserves stored before spring migration are related to the length of non-stop flight undertaken and only species that make very long-distance migrations depart with fat levels exceeding 40% (King 1972, Blem 1976). Shorebirds that breed close to their wintering grounds store little fat in spring (McNeil 1968, 1970, Baker 1975), and even some species, such as Bar-tailed Godwit that move a long distance from wintering to breeding grounds stored little fat before departure from Britain in spring (Evans & Smith 1975), possibly because they made a series of short flights between fattening grounds, rather than the long-distance non-stop flights made by, for example, Knots (Dick et al. 1976, Dick 1979), Sanderlings (Morrison & Wilson 1972, Ferns 1980) and Pacific Golden Plovers (Johnston & McFarlane 1967). These species carry very high fat loads in autumn and spring (Tables 25 and 26). Although many shorebirds require large fat reserves for successful migratory flights across natural barriers such as oceans, storage of large fat reserves is not necessarily a prerequisite for migration. There is evidence from passerines that individuals can vary their migration strategy depending on physiological state, success in competition and weather conditions (Rappole & Warner 1976). In shorebirds intraspecific variation in migration strategy is indicated in autumn migrant Semi-palmated Sandpipers (Page & Middleton 1972). Early migrants remained

at a stopover in Ontario for only a few days and continued short-distance migration with low fat reserves. Individuals migrating later stayed for much longer and deposited large fat stores (Tables 25 and 27), presumably for long-distance migration.

Protein Reserves

As fat is catabolised during flight, the total body weight of a migrating bird decreases. Pennycuick (1978) has proposed that during migratory flight birds should reduce their power output either by reducing the size of the pectoral muscles (by catabolising muscle protein) while flapping continuously or by alternating periods of flapping with increasingly long periods of gliding. If a reduction in pectoral muscle size occurs during migration, either premigratory hypertrophy of pectoral muscles leading to muscles of 'normal' size after migration should occur, or, if no premigratory hypertrophy occurs, pectoral muscles should be smaller after migration. Shorebirds probably do not undergo extensive premigratory hypertrophy of pectoral muscles or total lean weight in autumn, although this could be because birds were not sampled just before their departure. Indeed, shorebirds arriving at migration stopovers or wintering grounds in autumn have markedly lower lean weights than in the subsequent winter (Paper 3), and pectoral muscles are small. Loss of muscle protein may pose particular problems during autumn migration for first-year shorebirds, since their muscle growth is incomplete (Paper 3), and for species that undertake long non-stop flights to southern wintering grounds, e.g. Knot to Mauritania (Dick & Pienkowski 1979).

In spring, pectoral muscle hypertrophy involving increases in protein and increases in total lean weight is widespread in passerine birds before migration to the breeding grounds (e.g. Child 1969, Fry, Ferguson-Lees & Dowsett 1972, Ward & Jones 1977). In shorebirds also, increases in total lean weight prior to spring migration occur in both southern and northern hemispheres (Johnston & McFarlane 1967, McNeil 1970, Evans & Smith 1975; also see Paper 3). From this study it is clear that since pectoral muscles form a higher percentage of lean body weight in spring than winter, muscle hypertrophy is proportionately greater than the overall increase in lean weight in Dunlins, Sanderlings and Ringed Plovers in north-east England. Pectoral muscle hypertrophy accounted for 36% of the spring increase in lean dry body weight in Dunlins and 25% in Sanderlings.

Muscle protein is used during both autumn and spring migratory flight. However, in spring a large premigratory muscle protein reserve is needed for two additional reasons:

1) If severe weather or late snowmelt occurs after shorebirds have returned to their breeding grounds, protein reserves are needed during temporary starvation (Morrison 1975, Slagsvold 1976, Byrkjedal 1978, 1980, Marcstrom & Mascher 1979).

2) By increasing protein reserves before their arrival on the breeding grounds, arctic-breeding shorebirds minimise the amount of protein that they must accumulate on breeding grounds to regain condition lost on migration. Arrival in the best possible condition may be important in ensuring successful breeding, particularly

if food availability is limited in early summer in the arctic (Green, Greenwood & Lloyd 1977), since delays in the onset of breeding can jeopardise breeding success (Byrkjedal 1978).

Adequate protein reserves are known to be required for egg formation in some tropical birds e.g. Red-billed Quelea (Jones & Ward 1976) and Grey-backed Camaroptera (Fogden & Fogden 1979). Weight losses in tundra-nesting geese also involve losses of protein during egg formation and incubation (Ankney 1977). Although there is only very limited information on changes in the condition of shorebirds breeding in the arctic (Yarbrough 1970), adequate protein reserves are certainly needed for egg formation. Accumulation of some of these reserves before migration would allow a rapid response to suitable breeding conditions. This might be confirmed if the protein condition of birds was examined immediately after their arrival on breeding grounds. Male shorebirds may also require protein reserves during breeding since their time available for feeding may be limited by territorial defence and incubation (Holmes 1966, Ashkenazie & Safriel 1979), as in geese (Ankney 1977), and food intake can be less than daily energy requirements (Ashkenazie & Safriel 1979). However, any sex-differences in the size of protein reserves before or during migration may be very small, and none was detected in shorebirds before departure from north-east England in spring.

This pattern, of premigratory protein deposition in spring but not autumn, parallels the more extensive fat deposition in spring than autumn which probably occurs for similar reasons, namely that energy reserves

are needed if severe weather or late snow melt occurs on breeding grounds and that there will be a requirement for fat by females for egg formation, since eggs are rich in lipids (Carey, Rahn & Parisi 1980). Large fat reserves increase total body weight, which in turn increases the flight speed necessary to achieve maximum flight range (Pennycuick 1975, 1978). A reduction in flight time results, allowing birds to make most use of favourable weather conditions for migration. This may be important to the survival of shorebirds that make long over-water flights to breeding grounds e.g. Knots and Turnstones returning to Greenland (Morrison 1975, Dick et al. 1976, Dick 1979).

Moult

In many passerines, fat levels remain low during moult and glycogen is used as an energy store (Dol'nik & Blyumental 1967). Fat levels of adult shorebirds moulting wing and body feathers in autumn are also low. Moulting adult Dunlins (3% fat) and adult Grey Plovers (8% fat) at Teesmouth had much smaller fat reserves in autumn than non-moulting passage migrants. Adult Dunlins moulting on the Dutch Waddensee also maintained steady low fat reserves averaging 5% fat (Smit 1981) as did moulting Bar-tailed Godwits at Lindisfarne (Evans & Smith 1975). This pattern of little change in fat reserves during moult is common in migrant species (Payne 1972).

Moulting birds have raised daily energy requirements resulting from increased metabolic rate and reduced feather insulation (Payne 1972). In Canada Geese, which become flightless when moulting, Hanson (1962) found atrophy of pectoral muscles during moult, and Newton (1968) showed

evidence of heavy overnight protein demand in moulting Bullfinches. Since wing moult in migrant shorebirds often involves many primaries growing at once (Boere 1976), shorebirds, like geese, might be expected to utilise some of their pectoral muscle during moult to supply protein for more rapid feather growth. Adult Dunlins moulting at Teesmouth in September had smaller than 'normal' pectoral muscles (Figure 14). However Bar-tailed Godwits in active wing moult at Lindisfarne in autumn had pectoral muscles of a similar size to those of non-moulting birds in winter (Evans & Smith 1975). There is no further information on the effects of moult on shorebird muscle size.

Functions and Regulation of Nutritional Reserves during Winter

Fat Reserves

Whilst it has long been known that fat reserves are very important in enabling birds to survive during severe weather (King 1972), most studies have examined their function and regulation in small passerines. In most of these species winter fat reserves are limited to those sufficient for survival overnight and into part of the following day. This limitation occurs in both species experiencing low temperatures and long nights in midwinter (e.g. Newton 1969, Evans 1969a) and those in equatorial areas where seasonal changes in air temperature and photoperiod are small (e.g. Ward 1969). The size of the peak fat reserve is generally correlated with minimum air temperatures, or latitude (King 1972, Blem 1973, 1976), and Evans (1969) showed that air temperature was the ultimate factor controlling winter fattening in the Yellow Bunting, Emberiza citrinella.

In contrast, Bar-tailed Godwits at Lindisfarne carried sufficient fat reserves in midwinter to supply their energy requirements for several days (Evans & Smith 1975), as did other shorebirds in this study (Figure 32). Despite this difference, shorebirds in north-east England followed a similar seasonal pattern of fat storage to passerines wintering in areas where severe weather can occur: namely, fat deposition during early winter with a midwinter (December or January) peak in fat reserves followed by a decline until late February or March. These shorebirds usually reach peak fat reserves in late December, and in some species this level may be maintained during January (Knot) or until February (Golden Plover).

There are two hypotheses that can account for the midwinter peak in fat storage in shorebirds, and why fat reserves decline during late winter:

1) Both the midwinter fat level and the late winter decline are internally regulated. This hypothesis regards storage as an 'insurance' against difficulties in meeting food requirements (Evans & Smith 1975) so peak levels must be stored in advance of when they may be needed. The late winter decline in fat reserves is possible because the probability of weather conditions occurring that are severe enough to require fat catabolism gradually decreases after midwinter. Reduction in fat reserves must suppose that disadvantages exist in carrying large amounts of fat during winter, so the late winter decline results from a trade-off between these disadvantages and the requirement for 'insurance' against periods of inadequate food intake.

If fat is catabolised during severe late winter weather the regulated level will be regained when environmental conditions improve and there should be no year-to-year variation in either the widwinter peak level, or the level at any time during the late winter decline if the birds have not been "stressed" by bad feeding conditions.

2. Midwinter fat reserves are the maximum attainable and the late winter decline results from the obligate catabolism of fat reserves as a result of inadequate food intake. As discussed by Pienkowski, Lloyd & Minton (1979), this hypothesis suggests that feeding is inadequate to supply energy requirements after midwinter, mainly as a result of the depletion of food resources during the winter, coupled with reductions in prey activity and availability during cold weather (Smith 1975, Evans 1979, Pienkowski 1980a,b). Shorebirds should continue to deposit fat until they are unable to further do so. Year-to-year variations in early winter weather conditions mean that the midwinter peak fat reserves should show yearly variation in level and timing For the observed gradual decline in fat reserves to occur food intake must be almost continuously insufficient to balance energy requirements during later winter and only when improving weather conditions reduce energy requirements and increase prey availability in early spring can fat be again stored. As a result of yearly variations in the severity of weather conditions after midwinter, year-to-year variations should occur in late winter fat levels. This hypothesis also predicts that fat reserves will remain low after severe weather.

From the evidence presented earlier, it is clear that several shorebird species in north-east England regulate winter fat reserves, and several of the predictions arising from the hypothesis of regulated fat reserves can be confirmed.

Dunlins, Knots and Bar-tailed Godwits showed little evidence of year-to-year variation in the size of late winter fat reserves (Figures 5, 11, 12 & 17) indicating a programmed decline in fat reserves.

The crucial test of a regulated or obligate late winter decline in fat reserves, as pointed out by Pienkowski, Lloyd & Minton (1979) and Dugan et al. (1981) is whether fat is redeposited after its catabolism during severe weather. Reliable information is difficult to collect since it requires examination of birds before, during and after a period of severe weather. Ideally fat reserves should be followed in recaptured individuals since otherwise the biases of the departure or death of part of the population cannot be excluded. This precludes the examination of lipid indices by carcass analysis and the evidence presented below mainly refers to the total body weight of live birds. Much of a change in total body weight is due to a change in the weight of fat (Table 4).

Support for the regulation of winter fat reserves comes from Grey Plovers at Teesmouth during early 1979 (Dugan et al. 1981). Individual Grey Plovers are known to have survived, and to have returned to their normal total body weights after declining in early January to an estimated 35% below their normal lean weights (Paper 2). During this severe weather, these Grey Plovers must have catabolised all their fat reserves, and additionally used protein reserves extensively.

Dunlins at Teesmouth during the same severe weather in January and February 1979 also showed gains in estimated average lipid indices after apparent fat catabolism during severe weather (Paper 2: Figure 3). Weight changes of individual adult Dunlins that were weighed on various dates in January or February 1979 and again on 27 February 1979 confirm the pattern of weight loss followed by gain deduced from population estimates (Figure 29). After severe weather in January weights were low, but a respite in the cold spell in early February led to a partial regain of weight by 5 February. The normal spring decline in weight occurred through February. This led to the situation in which weight losses of individuals were greater between 5 February and 27 February than between 28 January and 27 February. Unfortunately no individuals were weighed on both 28 January and 5 February to confirm this recovery. Similar apparent weight gains after severe weather in late January were reported by Pienkowski, Lloyd & Minton (1979) for Dunlins from the Wash.

Grey Plovers are amongst the shorebirds that catabolise energy reserves most extensively during severe winter weather (Paper 2). As Grey Plovers can regulate winter fat reserves even in north-east England where winter weather conditions are amongst the most severe of anywhere in the wintering range of shorebirds (Dugan 1981a), most species of shorebirds should be able to do so. Available evidence suggests that this is the case. Additionally fat reserves are regulated at lower levels in other, milder, wintering areas, as occurs in other orders of birds (see Blem 1973, 1976). For example, Grey Plovers at Teesmouth carry over 20% fat in midwinter. The same species carried only 6.6% fat in equatorial Venezuela

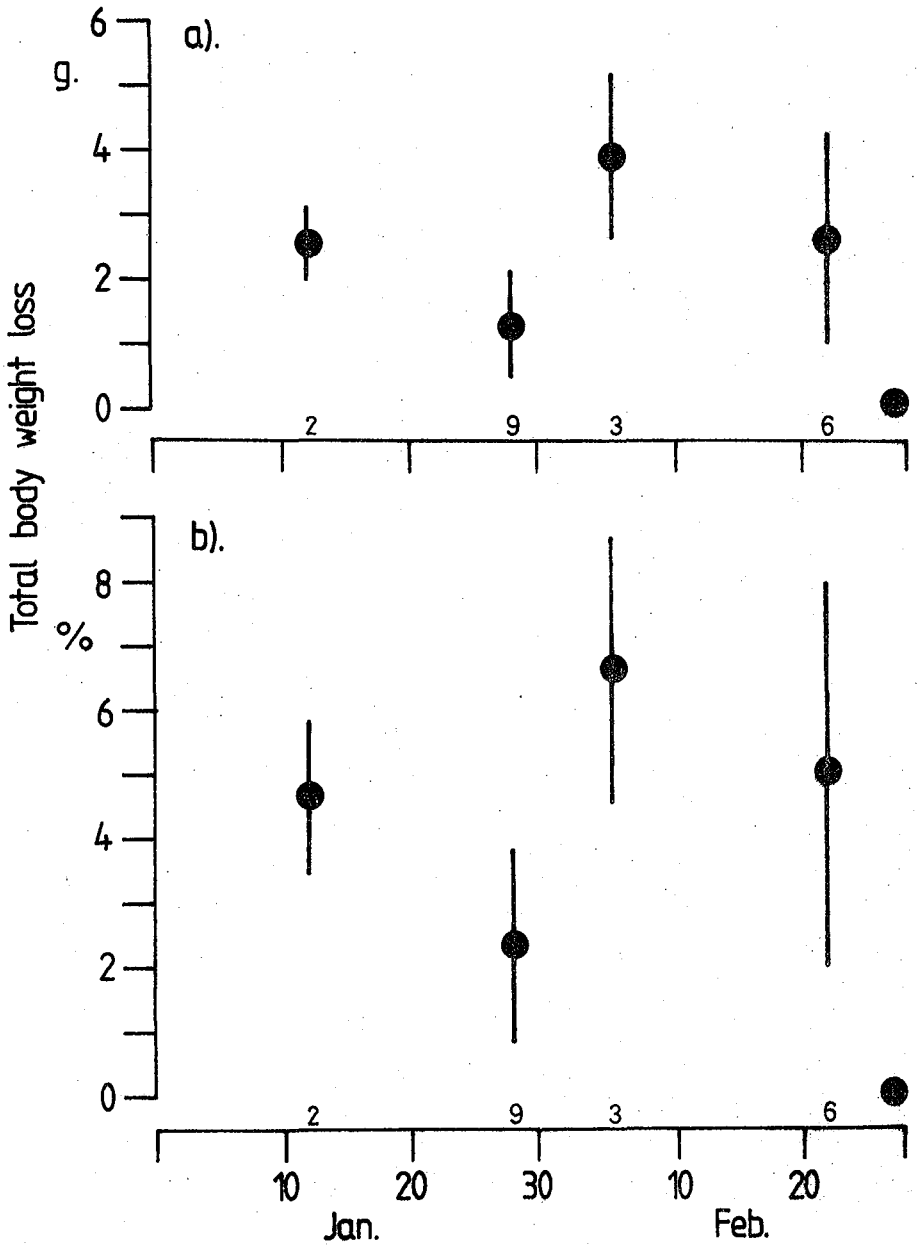

Figure 29: Weight changes of adult Dunlins weighed during January and February 1979 and again on 27 February 1979, expressed as a) weight (g.) lost and b) % weight lost. Each point shows the mean $\pm$ 1 standard error of the weight loss between date of first weighing and 27 February. Numbers indicate sample sizes.

(McNeil 1970), and 6.4% fat in South Africa (Summers & Waltner 1979) where 'wintering' birds experience austral summer. Pienkowski, Lloyd & Minton (1979) showed that on various estuaries within Britain midwinter total body weights of Dunlins were negatively correlated with midwinter air temperature, indicating the maintenance of a regulated fat reserve of greater size in wintering areas of harsher climates.

Some species also use fat reserves for long-distance movements in direct response to the onset of severe weather. This may affect the pattern of fat storage and occurs in Lapwings and Golden Plovers; species which mainly feed on pastures. Movements from northern Britain are generally south or south-westerly to western Britain, Ireland and exceptionally Iberia (Dobinson & Richards 1964) and Morocco (Smith 1965). The very large fat reserves carried by Golden Plovers in north-east England, even in mid-February (lipid index 25%) are likely to be adapted as much to long 'cold-weather' movements, as to their use as an energy reserve during severe weather by Golden Plovers that remained in north-east England and moved to feed in intertidal habitats (Paper 2). Evans (1976) found no evidence of similar 'cold-weather' migration in coastal shorebirds. One coastal shorebird that may respond to severe weather by moving south is the Redshank, although the evidence is slight. Some Redshanks were recovered in France during the severe winter of 1962/63 (Spencer 1964) but not during the 1978/79 severe winter or milder winters. However movement must have occurred during 1978/79 since numbers of Redshanks at Teesmouth at the start of severe weather in January 1979 decreased from 450 on 3 January to

225 on 15 January, the population remaining at this size until early March (Davidson 1980). This disappearance of 225 Redshanks occurred at a time of year when numbers are usually increasing. These birds are likely to have moved away from Teesmouth, since there was little evidence of Redshanks dying there in early January 1979, but their destination is unknown.

Cold-weather movements become increasingly unlikely the longer severe weather continues since fat and muscle protein reserves will become progressively more depleted so birds are less likely to carry sufficient reserves to allow flight to another estuary. A cold-weather movement has survival value only if the birds can reach feeding grounds where the weather conditions are less severe than on its source estuary and intraspecific competition is no greater.

Increasing evidence indicates the occurrence of complex movements of various shorebirds between different estuaries within Britain, and between Britain and other areas of western Europe (Evans 1976, 1981, Dugan 1979, 1981a). Whilst these movements are not made in direct response to the onset of severe weather they may occur in such a way and at such times as to minimise the effects of any severe weather period that occurs. If birds prepare for interestuarine movements during winter this could result in larger fat reserves being carried than would be maintained solely for use during severe weather, particularly in late winter when the probability of severe weather is low. The higher fat loads carried by Knots (12 - 15% fat) than other estuarine shorebirds during late winter (Figure 5) may indicate preparation for movement since many Knots are considered to be transient at Teesmouth

during the winter (Dugan 1981a).

Conversely, after an interestuarine movement, lipid indices can be depressed below those of conspecifics that have remained on an estuary for some time. This had occurred in Knots and Dunlins at Teesmouth in early December, when many birds carried depleted reserves, as a result of recent movement into Teesmouth, probably from the Wash. Individuals arriving at an estuary in mid or late winter must rapidly replace depleted reserves as insurance against severe weather occurring soon after their arrival.

The facility with which fat is stored during autumn and early winter, and is replaced in mid or late winter after mobilisation for migration or during severe weather suggests that shorebirds have little difficulty in achieving food intakes that allow a surplus to daily energy requirements to be stored as reserve fat. The rapid recovery of condition by Grey Plovers in early 1979 occurred when weather conditions, although slightly improved, were still severe (Dugan et al. 1981) and Grey Plovers are considered to be a species whose feeding is seriously affected by severe weather (Paper 2).

Since in autumn and early winter shorebirds must maintain a food intake rate high enough to not only balance their daily energy requirements but also to permit deposition of fat (and some protein) reserves, it might be expected that the time spent feeding during a tidal cycle and/or rates of biomass intake would be higher in autumn than after midwinter, when the gradually-mobilised fat reserves are available to supplement food intake, and daily energy requirements need only to be balanced rather than exceeded. However

Pienkowski (1980b) found no evidence of seasonal differences in the feeding rates or feeding times of Ringed Plovers or Grey Plovers in north-east England that could be attributed to these different requirements. On the Wash (Goss-Custard et al. 1977a) seven species of shorebirds fed for a greater proportion of the available time after than before midwinter. Higher energy requirements and lower prey availability after midwinter (see e.g. Evans 1979) must override the advantage of the regulated release of fat reserves. Also bird densities may be greater after midwinter, leading to interference in feeding (e.g. Goss-Custard 1976, 1977b).

Disadvantage of carrying large fat loads

The decline in fat reserves after midwinter in shorebirds in northern temperate latitudes and the small fat reserves maintained by shorebirds wintering in warmer areas indicate strong advantage in the maintenance of the smallest reserves necessary for survival. Circumstantial evidence for the disadvantages of carrying excess fat comes from the decline in fat reserves continuing throughout late winter until the onset of premigratory fattening, usually in March. Since there are energetic costs involved in fat deposition (Berthold 1975), birds regulating their fat reserves would not be expected to decrease reserves in late winter unless there was selective advantage in doing so.

Dick & Pienkowski (1979) suggest various costs of carrying large fat reserves. Those concerning the increased energetic costs involved in additional feeding to achieve a positive energy balance, and synthesis of depot fat from carbohydrate (Berthold 1975) are probably unimportant in view of the apparent ease with which fat is replaced after

its use on migration or during severe weather (Dugan et al. 1981). Other energetic disadvantages may be the work involved in carrying the extra weight of fat and the increased power required for flight at a given speed since the power required is proportional to Total Body Weight$^{3/2}$ (Pennycuick 1975) i.e. a small increase in weight requires a large increase in power to maintain flight speed. This may also be a reason why plovers have larger pectoral muscles than scolopacid shorebirds since plovers carry heavier fat loads and require larger muscles to generate sufficient power for efficient flight (Pennycuick 1978). Interspecific differences are discussed later. A further constraint on heavy fat loads may be a reduction in manoeuvrability and increase in take-off time, making individuals with high lipid indices vulnerable to predation from avian predators (Dick & Pienkowski 1979). Raptor predation can result in high mortality among the smaller species of wintering shorebirds (Page and Whitacre 1975) and even infrequent predation may be important in promoting flocking in shorebirds (Page and Whitacre 1975, Smith 1975, Stinson 1980). Since the response by most shorebirds to attempted predation by a raptor is to take off and fly in a tight flock (Page & Whitacre 1975, Davis 1980, pers. obs.) a grouping typical of prey in open habitats (e.g. Milinski & Curio 1975, Major 1978) individuals carrying heavy fat loads will be those that are most easily separated from the flock and so more liable to predation (Page & Whitacre 1975, Smith 1975). However, increased weight does permit faster flight (Pennycuick 1969, 1975), which could partly compensate for the disadvantage of reduced manoeuvrability, although this may be more important during long-distance migratory flight than for

short-distance predator avoidance.

Protein Reserves

In temperate wintering areas such as north-east England protein reserves, as measured by pectoral muscle size, do not show the midwinter peak found in fat reserves. Indeed pectoral muscle size generally remains steady throughout the winter (Figures 6, 10 and 18), and several pieces of evidence indicate that the reserves of protein they contain are regulated at levels which vary from species to species. The size of the pectoral muscles in shorebirds in north-east England during winter is correlated with the peak midwinter lipid index in each species (Figure 30). Since I have shown that the size of fat reserves is regulated in winter, it can be argued that the size of the protein reserves maintained by each shorebird is also regulated. Total lean weight varies with latitude (Paper 3). Lower lean weights were maintained in wintering areas where low temperatures did not occur compared with northern temperate wintering sites where cold stress was experienced (Paper 3). The final piece of evidence indicating regulation of pectoral muscle size is that in January 1979 Grey Plovers extensively mobilised lean body components, including pectoral muscle tissue in addition to their complete use of fat reserves during severe weather (Dugal et al. 1981, Paper 2). Muscle protein, as well as fat, must have been resynthesised when weather conditions improved since the average total body weight of the population had returned to its expected level within a month (Dugan et al. 1981). One marked individual Grey Plover is known to have followed this pattern, which therefore was not the result of selective death of birds in poor condition.

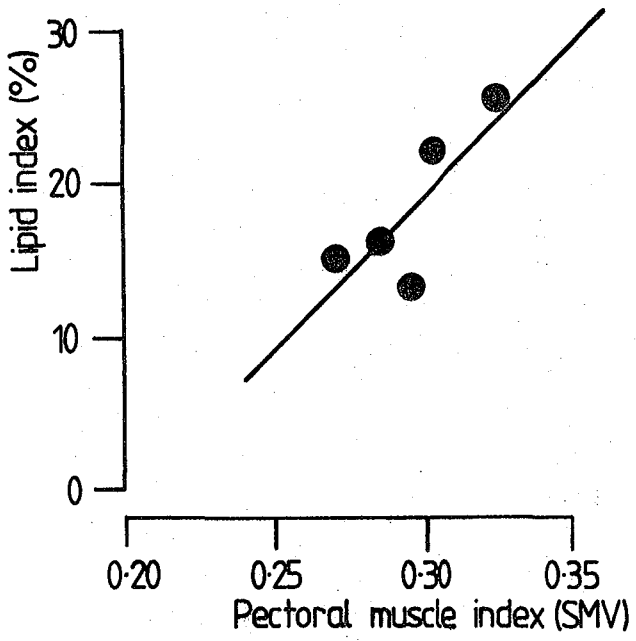

Figure 30: Relationship between the pectoral muscle size and lipid index of adult shorebirds during mid-winter in north-east England. Each point is the mean value for one species. Regression (——) is lipid index = 203.8 Pectoral muscle index - 42.1 $r_3 = 0.81$ $P < .10 > .05$.

Muscle protein is mobilised whenever animals, especially birds and mammals, starve, or their food intake is too low to supply sufficient amino-acids for protein turnover (Millward 1970, Evans & Smith 1975, Grammeltvedt 1978, Jones 1980). Its function as a nutritional reserve is different from that of fat which is catabolised whenever food intake is insufficient to balance energy requirements. Under conditions of high energy expenditure (e.g. high winds and low temperatures) fat can be catabolised without associated muscle protein catabolism, but it is unusual for protein reserves to be catabolised in the absence of fat reserve depletion (Evans and Smith 1975) unless the diet is protein deficient (Fisher 1972).

The use of pectoral muscles for protein reserve storage is widespread in birds including, in passerines, the Red-billed Quelea, Quelea quelea (Kendall, Ward & Bacchus 1973, Jones & Ward 1976), Grey-backed Camaroptera, Camaroptera brevicaudata (Fogden & Fogden 1979), Willow Warbler, Phylloscopus trochilus (Baggott 1975), and Yellow Wagtail, Motacilla flava (Fry, Ferguson-Lees & Dowsett 1972), and in non-passerines Canada Geese, Branta canadensis (Hanson 1962), Lesser Snow Geese, Chen c. caerulescens (Ankney 1977), Willow Grouse, Lagopus lagopus (Grammeltvedt 1978), Spruce Grouse, Dendragapus canadensis (Pendergast & Boag 1973), in addition to Bar-tailed Godwits, Limosa lapponica (Evans & Smith 1975) and various other shorebirds (this study). In many species the pectoral muscles are the main source of protein during starvation. In Dunlins starved in captivity (Appendix 1), losses of lean dry pectoral muscle tissue accounted for 40 - 50% of the total lean dry body weight losses. In starved Willow Grouse (Grammeltvedt

1978) over 30% of the total body weight loss was from pectoral muscles.

Other parts of the skeletal musculature can also contribute to the protein reserve. In geese, leg muscles form part of the protein reserve (Hanson 1962, Ankney 1977). Amongst shorebirds, Knots may have an alternative source of protein reserve to the pectoral muscles since pectoral muscle losses during starvation (Appendix 1) accounted for less than 15% of the total lean dry weight loss, and the pectoral muscles formed a smaller proportion of total lean weight than in most other scolopacid sandpipers (see Figures 7, 10, 15 and 18). Other sites of protein reserve storage in Knots have not been identified but may be the leg muscles, as in geese.

As during spring and autumn migrations, protein reserves may be mobilised during interestuarine movements by many shorebirds in winter and during movements by Lapwings and Golden Plovers in response to the onset of cold weather (e.g. Dobinson & Richards 1964, Smith 1965), when a dietary protein deficit arises or fat reserves become exhausted. Additionally, catabolism of pectoral muscle tissue during flight may occur for energetic reasons (Pennycuick 1978): as total body weight decreases as a result of fat catabolism, the power output needed from the pectoral muscles also decreases. Birds can reduce power output in two ways: either by reducing pectoral muscle size or by ceasing to flap continuously. Catabolism of pectoral muscles to reduce power output might explain the small pectoral muscles of Knots arriving at Teesmouth in early December, since

dietary protein deficit is unlikely to be a contributory factor. A direct flight from the Wash (their probable source estuary) would take at most 4 to 5 hours, assuming an average flight speed of 50 - 65 kilometres. hr^{-1} (McNeil 1970, Noer 1979). However the total weight loss during this flight may average only 5.5 g., a change of less than 4% of total body weight, so any change in pectoral muscle size should be very small. Starvation must be a contributory factor to muscle losses during very long migratory flights since some shorebirds can arrive in an extremely emaciated state, with no remaining fat reserves. Some are unable to recover e.g. in Mauritania (Dick & Pienkowski 1979).

Age-related Differences in Nutritional Condition

If winter peak fat levels are related to survival through periods of difficult feeding, age differences in rates of food intake could result in age-differences in regulated levels of fat and protein during the non-breeding season, and of the extent of catabolism of nutritional reserves during difficult feeding conditions.

Young birds generally achieve lower feeding rates than adults. Among shorebirds, Groves (1978) found that first-year Turnstones during autumn in Massachussetts had significantly lower feeding rates than adults. First-year Ringed Plovers on Lindisfarne had similar feeding rates to adults in early autumn, but when feeding conditions deteriorated in late autumn and winter, first-year birds had lower rates of food intake than adults (Pienkowski 1980b). Amongst other predatory birds, lower feeding ability in young birds than in adults has been widely reported in herons (Recher & Recher

1969a, Cook 1978, Quinney & Smith 1980) particularly during periods of food shortage (Siegfried 1971, 1972), and also in pelicans (Orians 1959), and Sandwich Terns except when food was superabundant (Dunn 1972). Young of some species compensated for lower feeding rates by increasing the proportion of available time spent feeding. This has been recorded in herons (Cook 1978), cormorants (Morrison, Slack & Shanley 1978), terns (Buckley & Buckley 1974 , D. Williard in Recher & Recher 1969a), but has not yet been shown in shorebirds. Lowered rates of food intake may also result from intraspecific aggression, but there is much interspecific variation in the effects of aggression on young shorebirds. Juvenile Turnstones were generally subordinate to adults in autumn (Groves 1978), and immature Oystercatchers on the Exe were 2 - 3 times more likely than adults to lose a mussel on which they were feeding (Goss-Custard 1980). Low foraging efficiency and inability to defend feeding areas against adults were suggested as major reasons who few first-year, but many adult, Grey Plovers at Teesmouth defended feeding territories (Townshend 1981a), which were advantageous during periods of severe weather (Townshend 1981a, Dugan 1981a). However, first-year migrant Semi-palmated Sandpipers instigated more aggression than adults, the attacker almost invariably winning (Harrington & Groves 1977). Similarly, in aggression over feeding sites in Bar-tailed Godwits, the attacker displaced the feeding bird, and adults or first-years were equally likely to attack or be attacked (pers. obs.). If young shorebirds are to ensure winter survival through regulated levels of nutritional condition, they should, on average, store larger fat reserves than adults in mid-winter,

since young birds are less able to achieve sufficient food intake during severe weather in late winter. There may not be age-differences in protein reserves because, if severe enough weather conditions occur to cause protein reserve mobilisation (e.g. during prolonged gales, or when the mud-flats are frozen), neither adults nor young birds would be able to feed. If any differences in regulated levels of protein reserves do occur, then young birds would be expected to carry larger reserves than adults.

The predicted differences in peak lipid indices hold for shorebirds wintering in north-east England. The peak mid-winter lipid indices of first-year Dunlins are higher than in adults and in Knots the lipid indices of first-year birds were consistently higher than those of adults. However, there were no age differences in peak fat reserves of Bar-tailed Godwits. First-year Grey Plovers at Teesmouth had as high or higher total body weights than adults during winter (Dugan et al. 1981). Since the lean weights of first-year shorebirds are lower than those of adults (Paper 3), it follows that first-year Grey Plovers must have been carrying larger fat reserves than adults during winter. The regulated decline in fat reserves after midwinter is faster in first-year than adult shorebirds, since by mid or late February there were no detectable differences in lipid indices. This greater regulated use of fat reserves may compensate for the lower feeding efficiency of young birds during the poor feeding conditions of January and February. If first-year shorebirds have higher peak fat levels (on average) than adult conspecifics despite lower feeding efficiency, this is further

evidence against food shortage in early winter controlling fat levels in mid-winter.

Most of the examples of age-related foraging differences refer to differences between 'average' adult and young birds. There is less information on age-related differences based on studies of individuals, although individual variation in foraging behaviour and feeding rates within an age-class is well-known in shorebirds (e.g. Norton-Griffiths, 1967, 1969, Recher & Recher 1969b, Goss-Custard 1970a, Heppleston 1971) and other orders of birds (e.g. Gill & Golf 1975, Davies 1976, Partridge 1976). In Grey Plovers during winter, some young birds had similar feeding rates to adults, but on average, young birds had lower intake rates (Dugan 1981a, Townshend 1981a). Additionally, some first-year Grey Plovers successfully defended feeding territories throughout the winter. The foraging efficiency of young birds should improve with experience during their first winter, although in some shorebirds, e.g. Oystercatchers feeding on mussels, Mytilus edulis (Norton-Griffits 1967, 1969) it can take several years for young birds to achieve full adult feeding efficiency. However, any improvement in feeding rates during winter may be insufficient to compensate for the increased energy requirements and decreased prey availability in late winter.

Since some first-year shorebirds have similar feeding efficiencies to adults but on average have lower efficiencies, a further prediction is that first-year shorebirds should show greater variation in regulated lipid indices than adults. This cannot be confirmed in this study because of large variations in the lipid indices of both age-classes, and may require very large samples to detect any differences. Large

samples of first-year birds are difficult to obtain since they usually form only a small proportion of the population (e.g. Furness & Baillie in press). Oystercatchers do not conform to the age-related differences in condition that occur in other shorebirds. No analyses of nutritional condition have been made on Oystercatchers but the total body weights of the small samples from Teesmouth conform to the seasonal patterns of weight on Morecambe Bay and the Wash (Figure 31), with adults steadily increasing weight between autumn and March (a unique pattern of winter weights in shorebirds wintering in Britain), and first-year birds following the normal pattern of a midwinter peak weight followed by a decline. Dare (1977) suggests that the weight pattern of adults is related to their early breeding season compared with arctic-breeding shorebirds, and is a consequence of their success in specialising on the abundant but difficult prey of large bivalve molluscs. First-year Oystercatchers have not fully acquired the feeding skills of adults (Norton-Griffiths 1967, 1969) and seem unable to achieve the fat storage pattern of adults. First-year Oystercatchers can suffer higher mortality during severe weather than most other shorebirds (see later), probably as a consequence of this inability to attain adult levels of fat storage. The much higher midwinter weights of first-year Oystercatchers on Morecambe Bay than the Wash and Teesmouth (about 45 g. difference between Morecambe Bay and the Wash)implies that first-year Oystercatchers may not store sufficient fat reserves on east coast estuaries for adequate late winter survival (cf. Redshanks in Paper 2). This requires further investigation.

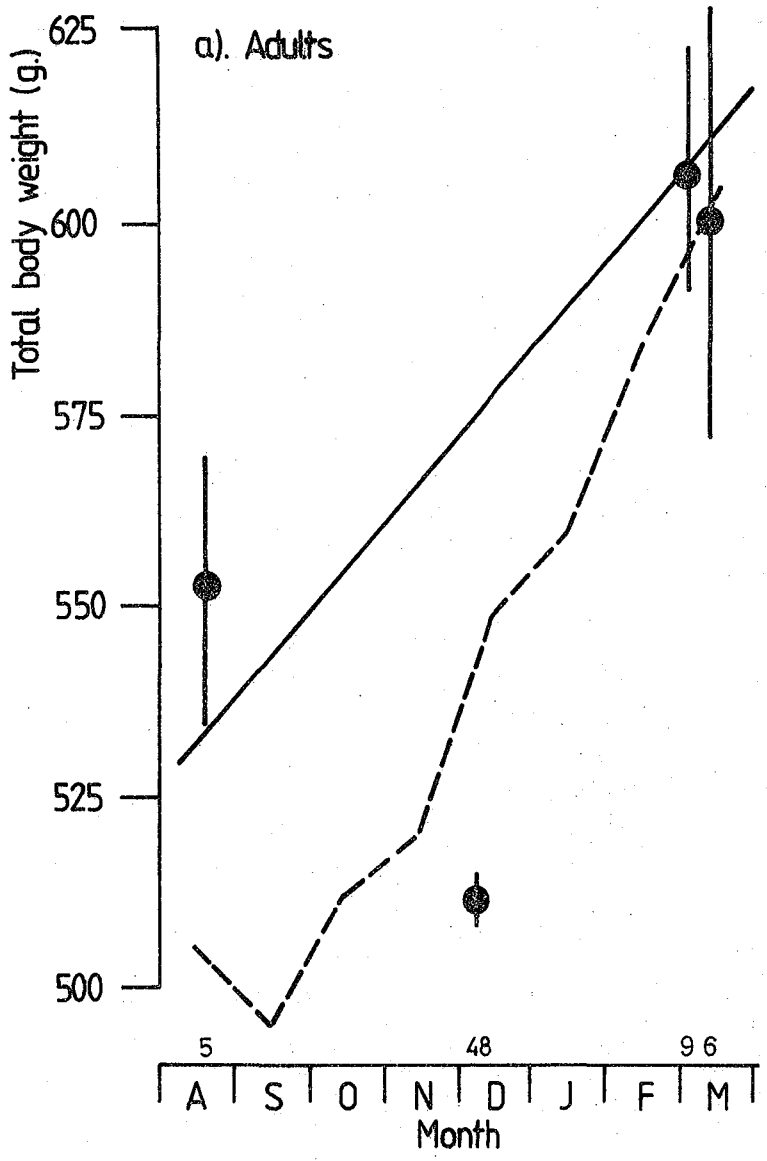

Figure 31: Total body weights of a) adult and b) first-year Oystercatchers at Teesmouth (●). Each point shows mean ± 1 standard error, and numbers indicate sample sizes. Also shown are mean weights on the Wash (---) from Branson (1979), and mean weights of mussel-feeders on Morecambe Bay (——) from Dare (1977).

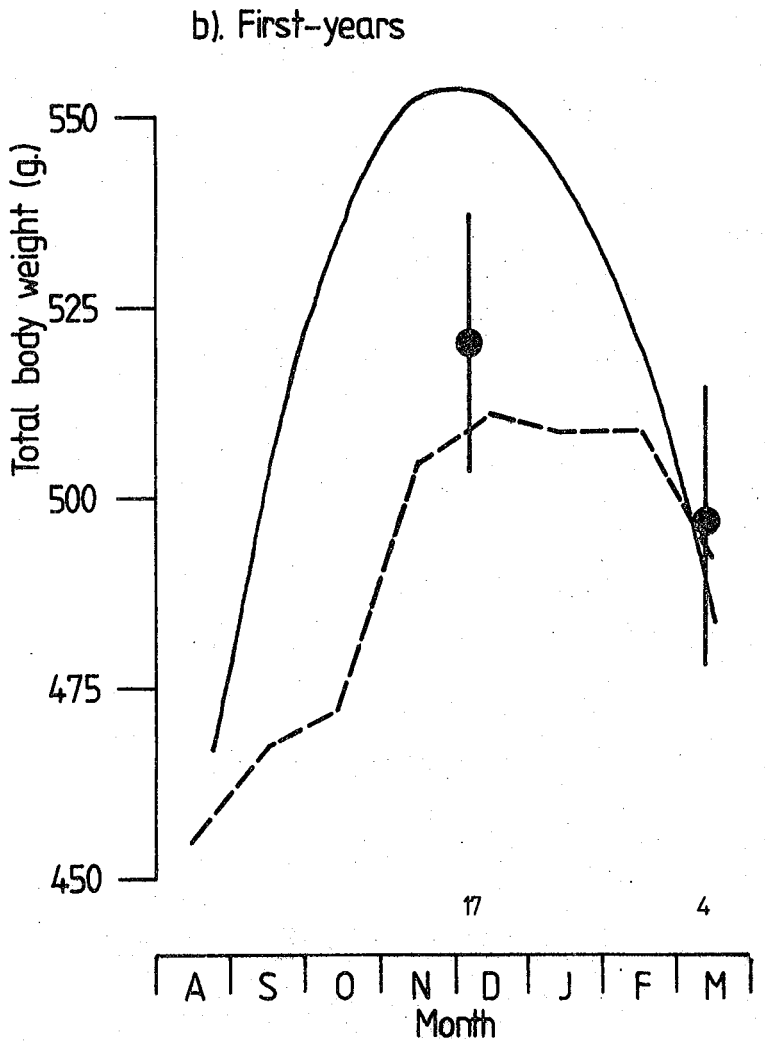
b). First-years
Total body weight (g.)
550
525
500
475
450
17
4
A
S
O
N
D
J
F
M
Month

Figure 31b

As predicted, there was little evidence of age-related differences in protein reserves. During winter, neither first-year Dunlins nor Bar-tailed Godwits had pectoral muscles that differed in size from those of adults. There was a trend for first-year Knots to have larger pectoral muscles than adults, but since parts of the Knot population are transient, the possibility that muscle size differences were an artefact of different migratory states of the two age-classes cannot be excluded.

First-year shorebirds are only a few months old in winter and their growth is incomplete. Within a sex, first-years had lower lean weights and lean dry weights than adults and these age differences in lean weights were still apparent in Dunlins in May. Pectoral muscles during autumn are also smaller in first-years than adults. Pectoral muscles of first-year Bar-tailed Godwits (Evans & Smith 1975) do not reach adult size until December or January. In other species such as Dunlin and Knot, pectoral muscle growth is more rapid, and by early winter there were no age-differences. First-years must carry similar protein reserves to adults by mid-winter to ensure survival through periods of severe weather in late winter. The similarity of the pectoral muscle size of adult and first-year Dunlins and Knots in early winter may be related to their movements between estuaries. Other differences in condition are related to age differences in the timing of the annual cycle. For example adult Dunlins in September carried low fat levels, probably due to moult and/or recent arrival at Teesmouth, whereas first-years were accumulating high fat levels for further migration. Age differences in the timing of spring pre-migratory fattening

also exist. In first-year Dunlins the late winter decline in lipid index continued until late March before pre-migratory fattening occurred, but adults started fattening in early March (Figures 11 and 12).

Interspecific Differences in Regulated Nutritional Reserves during Winter

All shorebirds need some nutritional reserves in winter as insurance for times when food intake is low or feeding impossible and for periods of high energetic cost when food intake is insufficient to balance energy requirements. Interspecific variation in the regulated size of fat and protein reserves could arise through differences in

a) the extent of reductions in the availability of food,

b) the energetic costs of thermoregulation,

c) whether long-distance movements are made in response to severe weather, and

d) residency or itinerancy during winter.

At each time of winter, the regulated level of nutritional reserves in each species results from the balance between the need for reserves for survival through periods of negative energy balance, often during severe weather, and the disadvantages of carrying extra weight. The amount of fat carried during the winter changes because the balance between the advantages and disadvantages of carrying large fat reserves varies seasonally. Those shorebirds that face the most frequent, longest or most severe negative energy balance should carry the largest midwinter fat reserves and have the largest pectoral muscles.

Weather conditions can reduce food availability and food intake by shorebirds in several ways. Severe weather

can affect the birds directly. Strong winds cause buffeting. For visual feeders this may prevent clear vision of cues given by prey at the surface and may also prevent directed movements to capture prey. Search areas of both visual and tactile feeders can be restricted by strong winds since foraging shorebirds can only feed successfully when facing into the wind. Under very windy conditions shorebirds may stop feeding and seek shelter. Strong winds also increase windchill, particularly in association with low air temperatures, causing a higher energy expenditure for thermoregulation (Gessaman 1973, Dugan 1981a), so that a higher food intake is needed to balance energy requirements. High windchills often occur simultaneously with reductions in prey availability and intake. Shorebirds that feed on the tide edge face reduced feeding times during gales when they are forced to regularly move up and down the shore to avoid waves. This particularly affects shorebirds feeding on exposed coasts. Mutual interference can also reduce prey availability and intake when birds are forced to form tight flocks during severe weather.

Similar severe weather conditions reduce food intake by shorebirds through their effects on invertebrate prey. Low substrate temperature, usually associated with low air temperature, reduces the activity of many invertebrates and some also move deeper into the substrate. Cues appear less often at the surface for visual feeders and a smaller percentage of prey lie within reach of tactile feeders. High winds, by drying the substrate surface, cause similar changes in invertebrate behaviour as low temperatures. However strong wave action can sometimes increase prey availability by forcing some invertebrates into the water column. Changes

in prey availability and energetic costs of foraging caused by severe weather are further discussed by Evans (1976, 1979), Pienkowski (1980a, b) and Dugan (1981a).

The energy balance of different shorebirds, even those feeding in mixed groups on the same mudflat, is most affected by different weather conditions, due to differences in diet, foraging behaviour, movements and morphology (Dugan et al. 1981, Paper 2). As a result of this variation, shorebirds must store different sizes of nutritional reserves if they are to provide adequate insurance against severe weather. Most weather conditions that affect the energy balance of shorebirds (e.g. low temperatures, gales and snowcover) become most severe during midwinter (Dugan 1981a) so that seasonal patterns of reserve storage are similar in most shorebirds.

The factors that can lead to the storage of nutritional reserves are listed in Table 28. Table 29 summarises those factors that cause each shorebird to store nutritional reserves and the size of the reserves carried by shorebirds in north-east England.

Plovers, as predicted by Pienkowski (1980a), carry larger fat and protein reserves than scolopacid Sandpipers (Table 29). This is mainly a consequence of Plovers being chiefly, if not wholly, visual feeders. Weather-induced decreases in prey availability affect estuarine plovers (e.g. Grey Plovers and Ringed Plovers) at higher temperatures than sandpipers since plovers rely on surface cues for prey location (Pienkowski 1980a, b) whereas touch-feeding sandpipers can take prey from below the substrate surface and so are unaffected by decreases in surface prey availability. Moreover on some estuaries Grey Plovers have difficulty in

Table 28. Factors that may lead to an increase in the size of fat and protein reserves needed by shorebirds during winter[a]

Factor	Reason(s) for reserve catabolism
Morphological	
Small body size	Higher BMR/unit weight; greater surface area: vol. ratio.
Long legs	Buffeting by wind - move from preferred feeding areas.
Short bill (tactile feeders)	Prey unavailable when deeper in substrate
Foraging	
Obligate visual foraging (e.g. plovers)	Reduced food intake when prey activity decreased; buffeting prevents clear vision, or rapid directed movements for prey capture.
Foraging on exposed substrate only	Feeding bad or impossible when mudflats frozen or prey activity low.
Preferred foraging on fields	Feeding impossible when fields frozen or snow-covered.
No foraging at night	Temporary starvation during overnight roosting.
No shelter on feeding areas.	High windchill unavoidable.
Unpredictable decreases in prey availability	Low food intake when finding new feeding areas.
Movements	
'Preprogrammed' movements between estuaries[b]	Metabolic requirements of flight.
Cold weather movements	Metabolic requirements of flight.
Irregular movements by transients (see Sanderling)	Metabolic requirements of flight.

[a] All shorebirds can use fat reserves during periods of high windchill.

[b] Reserves may be only stored shortly before a 'preprogrammed' movement rather than maintained as an 'insurance' against severe weather.

Table 29. Interspecific differences in regulated fat and protein reserves of adult shorebirds in winter in north-east England, and the main factors requiring storage of nutritional reserves. Predictions are made for shorebirds not examined in this study.

Species[a]	Mean Peak lipid index (%)	Pectoral muscle size (SMV)	Factors requiring reserve storage (from Table 28)[b]
Golden Plover	25+	.32	Visual foraging, fields, cold weather movements.
Lapwing	(25+)[c]	?	As Golden Plover.
Snipe	(20-25)	?	Field feeding, small body size.
Grey Plover	22	.30	Visual foraging, exposed substrate, long legs.
Ringed Plover	(20-25)	?	Visual foraging, exposed substrate, small body size.
Sanderling	c.20	.27	No shelter,unpredictable decreases in prey, irregular movements, short bill, small body size. size.
Turnstone	(15-20)	?	No night feeding, small body size.
Knot	15+	.29	Preprogrammed movements, short bill, small body size.
Curlew	(15)	.28	Some field feeding, long legs.
Dunlin	15	.27	Short bill, small body size.
Bar-tailed Godwit	13	.29	Long legs, tide edge feeding difficult during gales.
Purple Sandpiper	(5-10)	?	Wave action (little reserve needed).

[a] Species are listed in descending order of fat reserve size. Redshank and Oystercatcher are omitted because their patterns of condition differ from other shorebirds (see text and Paper 2).

[b] All shorebirds can require fat reserves for periods of high windchill. Highest windchills are faced by species that feed on open coasts and exposed mudflats.

[c] Brackets indicate predicted values of lipid indices.

feeding successfully on open mudflats (Dugan et al. 1981). The 'stand and wait' foraging method used by plovers appears particularly susceptible to the effects of buffeting during gales. Buffeting prevents visual location of feeding cues and makes the rapid movements for prey capture difficult to direct accurately.

In addition to the foraging problems resulting from buffeting, field-feeding plovers such as Golden Plovers and Lapwings have periods of no available food when fields become frozen or snow-covered. Fields freeze more frequently than do intertidal habitats during winter. When fields become untenable, Lapwings and Golden Plovers must move either to the coast or to milder conditions further south or south-west (Dobinson & Richards 1964, Smith 1965). These long-distance movements require a large fat reserve. Frozen fields and cold weather movements can occur in late winter so Golden Plovers, unlike other shorebirds, need to maintain large fat reserves until at least mid-February (Table 30). Larger pectoral muscles than other shorebirds (Table 31) may also be needed for long distance cold weather movements. During severe weather Grey Plovers and Golden Plovers catabolised both fat and protein reserves more extensively than did sandpipers (Paper 2).

Amongst Scolopacid Sandpipers, reductions in food intake as mud temperature decreases have been recorded for Knots (Goss-Custard et al. 1977a), Bar-tailed Godwits (Smith 1975), Redshanks (Goss-Custard 1969) and Curlews (Townshend 1981a) feeding on a variety of invertebrates. However, these reductions in food intake often start at lower

Table 30. Comparison of the late winter lipid indices of Golden Plovers and other adult shorebirds

Species	Date	n	Lipid index (%)[a]	P[b]
Golden Plover	8.2.78	10	24.2 ± 0.8	
Dunlin	9.2.78	15	9.7 ± 0.6	<.001
Knot	9.2.78	9	13.2 ± 0.8	<.001
Bar-tailed Godwit	9.2.78	3	11.3 ± 3.9	<.010
Grey Plover	9.2.78	6	14.5[c]	--

[a] Values are mean ± 1 standard error.

[b] Significance of difference from Golden Plover value (Student's t).

[c] Estimated value.

Table 31. Comparison of pectoral muscle size of Golden Plovers and other adult shorebirds in February.

Species	Date	n	SMV[a]	P[b]	% LW[a]	P[b]
Golden Plover	8.2.78	10	.323 ± .008		7.75 ± 0.08	
Dunlin	9.2.78	15	.281 ± .005	<.001	5.75 ± 0.07	<.001
Knot	9.2.78	9	.303 ± .009	n.s.	5.60 ± 0.09	<.001
Bar-tailed Godwit	9.2.78	3	.278 ± .024	n.s.	6.19 ± 0.05	<.001

[a] Values are mean ± 1 standard error.

[b] Significance of difference from Golden Plover value (Student's t).

temperatures than for plovers (Pienkowski 1981a). Additionally, most Sandpipers can partially compensate for reduced prey availability by changing from visual to tactile feeding and by changing the prey species taken (Smith 1975, Evans 1976). Periods of negative energy balance should occur less frequently and be less severe in sandpipers than plovers so Sandpipers need to store smaller fat protein reserves.

Strong winds will affect sandpipers in similar ways to plovers, except that most sandpipers can continue to forage during gales by changing to tactile feeding (Goss-Custard 1976, Evans 1976). Buffeting does affect long-legged Scolopacids: Bar-tailed Godwits sometimes do not attempt to feed and remain on roosts during severe gales (Evans 1976). Tide-edge feeding by Godwits is restricted during gales by strong wave action that reduces visibility when birds are feeding visually and that repeatedly forces birds to move away from feeding locations (Evans 1976, Wishart & Sealy 1980). Some Curlews move from mudflats to fields during gales (Townshend 1981b). Both plovers and sandpipers feeding on open mudflats face high windchills when gales are accompanied by low temperatures. Long-legged sandpipers such as Bar-tailed Godwits, Curlews and Redshanks should face higher windchills than short-legged shorebirds such as Dunlins and Knots. However Dunlins and Knots are small shorebirds and because metabolic rate varies with body weight$^{0.75}$, the higher metabolic rates per unit weight of these small shorebirds may result in similar extra fat storage to that needed by long-legged species facing higher windchills.

Redshanks encounter similar high windchills and reductions in prey availability as other long-legged Scolopacids, but Redshanks may not be able to maintain regulated levels of nutritional reserves in north-east England (Paper 2).

Many Knots move between estuaries during winter (Dugan 1981a). These itinerant individuals may need to store fat and protein for interestuarine flights in addition to the reserves needed for survival during severe weather, so Knots may store larger reserves than other Scolopacids. However, any additional reserves might be stored only shortly before departure on an interestuarine flight because of the disadvantages of carrying additional weight, so the reserves carried by Knots could vary between the same size and larger than other Scolopacids.

Knots generally carried similarly-sized or larger fat and protein reserves than Dunlins. In comparisons of the two species collected on the same days, adult Knots had significantly higher lipid indices on three of four days during winter, and first-years on one of two days (Table 32). Adult Knots had larger pectoral muscle indices than Dunlins in comparisons of birds sampled on the same days (Table 33a) (Difference between mean indices of Knots and Dunlins, paired comparison $t_2 = 12.01$ $P < .02$), although examination of separate days showed that both adult and first-year Knots had significantly larger pectoral muscle indices only on 9 February 1978. Pectoral muscles of Knots generally formed a smaller proportion of total lean weight than in Dunlins (Table 33b), although only significantly so in first-years in November 1977. Since pectoral muscle size in relation to SMV is larger in Knots than Dunlins (Table 33a), it follows that lean body components

Table 32. Lipid indices of Dunlins and Knots collected at Teesmouth on the same days.

	Lipid Indices (%)		
	Dunlin	Knot	P (Student's t)
Adults			
10 Nov. 1977	5.6 ± 0.7 (5)	10.0 ± 1.1 (4)	<.025
9 Feb. 1978	9.7 ± 0.7 (15)	13.2 ± 0.8 (9)	<.01
5 Feb. 1977	10.0 ± 0.9 (6)	13.6 ± 0.5 (3)	<.01
29/30 Jan. 1973	12.0 ± 1.7 (2)	12.2 ± 0.5 (20)	n.s.
First-years			
10 Nov. 1977	7.4 ± 0.9 (5)	13.7 ± 3.7 (6)	n.s.
9 Feb. 1977	8.5 ± 0.6 (11)	15.4 ± 0.9 (6)	<.001

Figures are $\bar{x} \pm 1$ S.E. (n).

Table 33. The pectoral muscle size of Dunlins and Knots collected at Teesmouth on the same days.

	Dunlin	Knot	P (Student's t)
a) Pectoral Muscle Index (SMV)			
Adults			
10 Nov. 1977	.261 ± .019 (5)	.286 ± .006 (4)	n.s.
5 Feb. 1977	.270 ± .009 (6)	.300 ± .012 (3)	n.s.
9 Feb. 1978	.281 ± .005 (15)	.303 ± .009 (9)	<.05
First-years			
10 Nov. 1977	.281 ± .006 (5)	.292 ± .013 (6)	n.s.
9 Feb. 1978	.281 ± .007 (11)	.319 ± .003 (6)	<.001
b) Pectoral Muscle Index (% LW)			
Adults			
10 Nov. 1977	5.85 ± 0.14 (5)	5.06 ± 0.11 (4)	n.s.
5 Feb. 1977	5.41 ± 0.04 (5)	5.53 ± 0.17 (3)	n.s.
9 Feb. 1978	5.75 ± 0.07 (15)	5.60 ± 0.09 (9)	n.s.
First-years			
10 Nov. 1977	6.06 ± 0.05 (5)	5.34 ± 0.18 (6)	<.02
9 Feb. 1978	5.77 ± 0.10 (11)	5.59 ± 0.07 (6)	n.s.

Figures are $\bar{x} \pm 1$ S.E. (n).

other than pectoral muscles must form a larger proportion of total lean weight in Knots than Dunlins. As yet little is known of the differences in reserve storage by resident and itinerant shorebirds.

Midwinter sea temperatures are generally higher than air temperatures (e.g. Dugan 1981a). This means that coastal beaches are less subject to freezing than estuarine mudflats, so Sanderlings feeding on coastal sandy beaches are less affected by temperature-induced reductions in prey availability than estuarine shorebirds. Scouring by gales and strong wave action often results in localised depletion of available prey, although scouring and formation of wrack beds can also result in increased prey availability (Myers, Connors & Pitelka 1979, Evans 1981). Sanderlings respond with abrupt changes in foraging behaviour and switches of foraging location after storms (Myers, Connors & Pitelka 1979, Myers 1980, Myers & McCaffery 1980). Strong wave action also reduces feeding time by increasing the time Sanderlings feeding on the tide edge spend running from waves (Myers 1980, Brearey 1981). There is little shelter available to Sanderlings on sandy beaches. When gales are accompanied by low temperatures Sanderlings face high windchills and increased energy requirements for thermoregulation at times when the sudden prey depletions occur. Sanderlings need larger fat reserves than similarly-sized estuarine sandpipers such as Dunlins which can feed in shelter during gales, do not face unexpected prey depletions and seldom need to switch feeding location. Compared with Dunlins, Sanderlings carried larger fat reserves in late winter (Figure 8).

Turnstones forage on both rocky and sandy coasts

(Harris 1979, Brearey 1981, Baker 1981). Turnstones should need smaller fat reserves than Sanderlings because they can forage in shelter amongst rocks during gales and the availability of rocky shore prey may decrease less than on soft substrates since prey on rocks cannot move deeper into the substrate in response to low temperatures. Turnstones can also feed throughout the tidal cycle on wrack beds above the high water mark. However Turnstones are the only shorebirds wintering in north-east England that do not feed at night (Evans 1976, Baker 1981, Brearey 1981). In midwinter Turnstones roost for up to 18 hours overnight and need a fat reserve as an energy source during overnight roosting, as do many passerines (e.g. King & Farner 1966, Evans 1969a, Newton 1969, Ward 1969, Taitt 1973). There is little evidence of protein reserve mobilisation during overnight roosting (Appendix 1) so Turnstones do not need larger protein reserves than shorebirds that do not feed at night. In November, first-year Turnstones at Teesmouth had pectoral muscles the same size as other shorebirds (Table 34). Recent arrival at Teesmouth may have been the cause of the low fat reserves of Turnstones in November (Table 34). Why Turnstones do not feed at night is not clear, since even plovers, which feed only visually, can feed successfully at night (Pienkowski 1980b, Dugan 1981b).

Purple Sandpipers are confined to rocky shores and so face similar feeding conditions to Turnstones, but Purple Sandpipers can feed at night (Atkinson et al. 1981). Rocky shores seldom freeze in cold weather so their food, mainly littorinids and dog whelks (Feare 1966), is seldom unavailable and they can avoid high windchills by moving

Table 34. Nutritional condition of first-year Turnstones compared with other first-year shorebirds in north-east England.

	Turnstone	Dunlin	Knot	Bar-tailed Godwit
n	14 Nov 75/ 23 Nov 76 4	10 Nov 77 5	10 Nov 77 6	November 7
Lipid Index (%)	3.61 ± 0.39	7.38 ± 0.85**	13.68 ± 3.69*	9.40 ± 0.81***
Pectoral Muscle Indices:				
a) SMV	0.258 ± 0.016	0.281 ± 0.006	0.292 ± 0.013	0.261 ± 0.009
b) % LW	6.45 ± 0.32	6.06 ± 0.05	5.34 ± 0.18*	5.26 ± 0.10*

Notes: 1. Values are mean ± 1 standard error. Bar-tailed Godwit data from Evans & Smith (1975).

2. Significant differences from the condition of Turnstones (Student's t-tests) are:

*** $P < .001$, ** $P < .01$, * $P < .05$.

into shelter amongst rocks, so large fat reserves are not needed. Only strong wave action is known to cause reductions in food intake by forcing birds to abandon feeding at lower shore levels and to repeatedly move away from waves (Feare 1966). Purple Sandpipers can overwinter further north than other shorebirds, being the only shorebird wintering in Greenland (Morrison 1976) and the commonest in Iceland, the east coast of Canada and Sweden (Morrison 1976, Wilson 1981, O. Pehrsson, pers. comm.). Unlike other shorebirds in eastern Britain, Purple Sandpipers in eastern Scotland maintain a steady low weight throughout the winter (Atkinson et al. 1981). This absence of extensive fat storage in midwinter is more typical of shorebirds wintering in the tropics and southern hemisphere (McNeil 1970, Thomas & Dartnall 1970, Summers & Waltner 1979).

Oystercatchers, particularly those that specialise on mussels, have an abundant food supply (once the specialised feeding techniques have been learnt (Norton-Griffiths 1967, 1969)) whose availability, like that for Purple Sandpipers, is not reduced by low temperatures. Indeed availability can temporarily increase in very cold weather when bivalves become moribund (Dare & Mercer 1973). Only buffeting from gales and high windchills are likely to cause any nutritional reserve catabolism by adult mussel-feeding Oystercatchers. Individuals that specialise by feeding on earthworms on pastures are more seriously affected by severe weather (Heppleston 1971) since, like Lapwings and Golden Plovers, they must move from their preferred feeding grounds during hard frosts and snowcover. Abundant available food in winter means that many adult Oystercatchers need store little fat as an insurance

against severe weather and can steadily increase their fat reserves throughout the winter as an adaptation to an early breeding season (Dare 1977).

Using formulae for daily energy requirements derived by Kendeigh, Dol'nik & Gavrilov (1977), interspecific variation in fat reserves can be expressed as survival times at different temperatures when the only energy source is stored fat. These values are unlikely to be actual survival times because the effect of windspeed increasing energy requirements is not taken into account and very cold calm conditions seldom occur during severe weather (Dugan 1981a). Conversely some feeding is often possible even during severe weather so that survival times would be longer than predicted.

In midwinter at temperatures between $0^{o}C$ and $5^{o}C$ when many invertebrates reduce their activity and availability to shorebirds (Evans 1979, Pienkowski 1980a, b) the survival times of sandpipers (2 - 4 days) are shorter than those of plovers (4½ - 9 days) (Figure 32a). The survival times of Ringed Plovers may be underestimated since they were calculated from an estimated lipid index of 25%. To achieve the same survival times as Grey Plovers, Ringed Plovers would need a lipid index of 40% because their metabolic rate per unit weight (0.63 kcals. g. LW^{-1} at $0^{o}C$), calculated from Kendeigh, Dol'nik & Gavrilov (1977), is higher than that of Grey Plovers (0.36 kcals. g. LW^{-1} at $0^{o}C$). Peak midwinter lipid indices of Ringed Plovers have not been examined.

Although Turnstones store fat as an energy source for overnight roosting their midwinter fat reserves are sufficient for survival for 3 days at $0^{o}C$ (Figure 32a), about four times larger than the reserve needed for one night-time period.

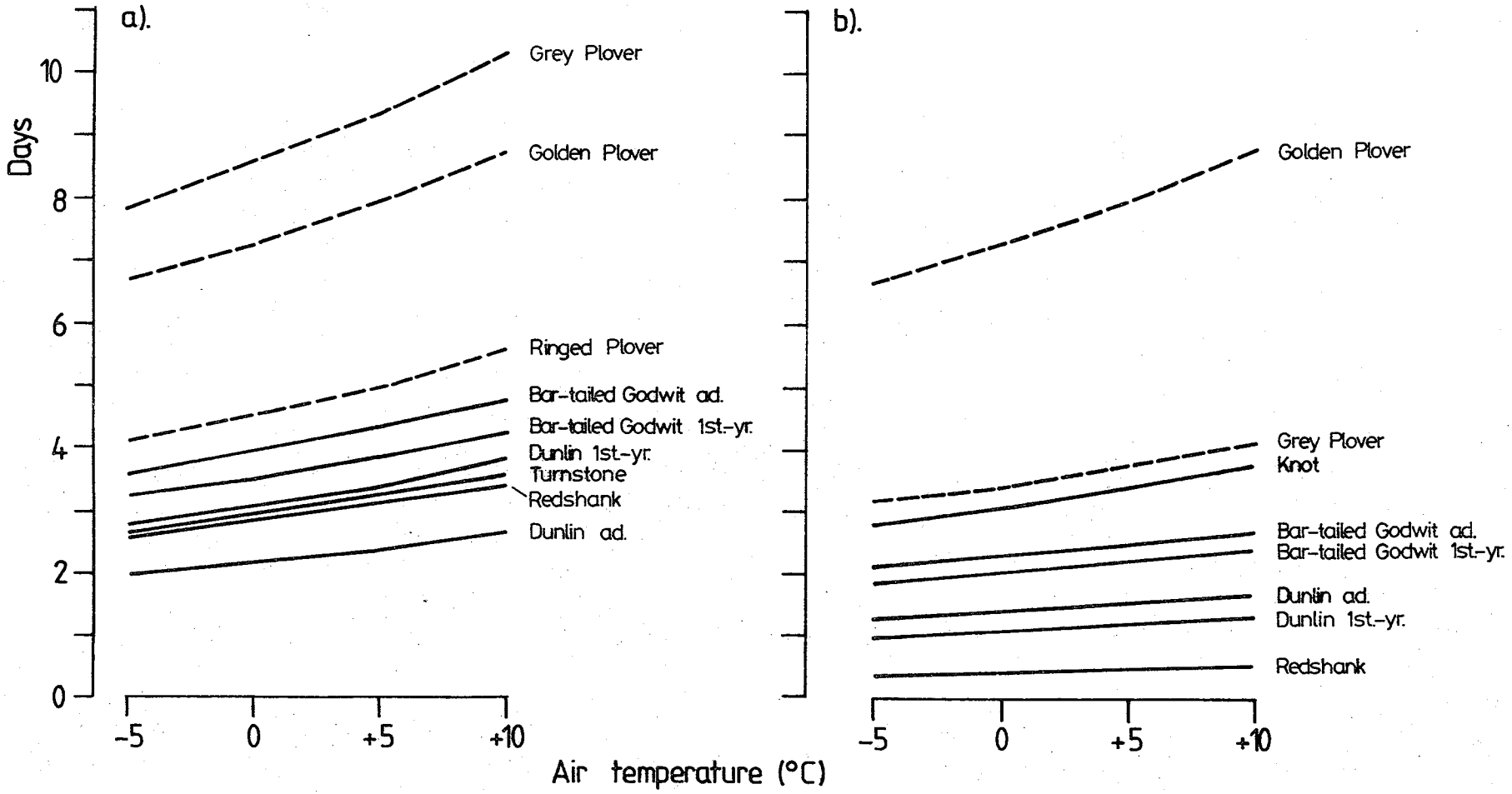

Figure 32: Predicted survival times at different air temperatures of plovers (----) and sandpipers (——) in north-east England using only fat reserves, during a) mid-winter and b) mid-February, calculated from Kendeigh, Dol'nik and Gavrilov (1977). Values for Ringed Plover and Turnstone are based on estimated lipid indices. Lipid indices of Redshanks are from Paper 2.

Therefore some fat may be stored by Turnstones as insurance against periods of daytime energy deficit. In this respect Turnstone differ from passerines which store only enough fat for survival for one night (e.g. Evans 1969a).

In mid-February (Figure 32b) survival times are shorter than during midwinter because smaller fat reserves are carried. As in midwinter plovers can survive for longer than sandpipers using only stored fat. The long survival of Golden Plovers in February reflects the large fat reserve needed for long-distance cold weather movements. Similarly the longer survival by Knots than other sandpipers may reflect fat storage for interestuarine movements rather than only for survival during severe weather. Even in February when shorebirds carry their smallestwinter fat reserves, most species can survive without feeding for at least one day (Figure 32b). The exceptions are Redshanks which carry sufficient fat reserves for survival at $0^{o}C$ for only about 10 hours.

<u>The value and limitations of body composition measurements for examining seasonal changes in nutritional condition and the effects of severe weather</u>

This study has shown clearly how nutritional reserves function as adaptations to overwinter survival in harsh climates. However two problems hinder further development of this research area:

1) In assessing nutritional condition, more rapid methods than the time-consuming techniques of laboratory analysis of estimating fat and protein reserves are required, so that more and larger samples can be examined.
2) In the interpretation of seasonal changes and levels of nutritional condition,

a) the effects of population turnover must be taken into account, and

b) resident and transient individuals in a sample must be identified.

Possible solutions to these problems are discussed below.

Estimation of the nutritional condition of live birds

Various techniques of estimating nutritional condition (chiefly fat reserves) have been devised (McNeil 1969, McNeil & Cadieux 1972b, Page & Middleton 1972, Mascher & Marcstrom 1976, Owen & Cook 1977, Bennett & Bolen 1978, Bailey 1979, Davidson 1979, Pienkowski, Lloyd & Minton 1979, Owen 1981, Appendix 2), but none have, so far, proved sufficiently accurate for widespread use for shorebirds. Furthermore, none are suitable for the estimation of absolute values of fat and protein reserves in individuals rather than in populations, although they can be used to examine the relative changes with time in the condition of an individual bird. However, this yields little more information than that from the total body weight changes of individuals. Estimates of fat reserves in live shorebirds have usually been made by subtracting from total weights the estimated lean weights, calculated from body size parameters such as wing-length or bill-length. This technique is accurate only if lean weight or body size parameters do not vary with season. However, lean weight varied by up to 10% between samples of Dunlins during winter in this study, and in spring lean weight steadily increases, particularly rapidly before migration. The problem is even greater in young birds, because they are still growing during autumn and the first

half of winter. Also, accurate estimates of fat can be made only when lean weights are 'normal' for the season concerned. This limits the value of estimates in calculating loss of condition during severe weather, or during or after migration, when it is likely that protein reserves have been catabolised. Some techniques now exist for estimating protein reserves independently from fat reserves (Davidson 1979) and a combination of the two estimates could be developed for future examination of losses of condition. Quantified losses of nutritional condition can be made at present only using carcass analysis.

Total body weight

Instead of estimating the fat and protein reserves of live birds, changes in condition can be assessed from total body weights. However the use of total body weight as a condition estimator is subject to several limitations. Although mean total body weights of samples of live birds can indicate relative differences in the average fat reserves carried by a population, total body weights give no information on the size of protein reserves. Because population turnover during the winter can lead to changes in the mean body size and lean weight of a population, total body weights should be corrected to a standard body size otherwise some apparent changes in fat reserves resulting from body size changes could arise. However standardising total body weights does not eliminate error caused by seasonal changes in the size of protein reserves and total lean weights. Changes in the total body weight of individuals (e.g. Figures 26 - 29) are subject to fewer errors and yield information on relative changes in fat reserves. In most cases the use of

total body weights should be restricted to these within-winter individual weight changes. The limitations on the value of total body weights as condition estimators mean that total body weight cannot be used as a complete substitute for carcass analysis.

Population turnover

I have shown for several shorebirds that apparent seasonal changes in nutritional condition can result from sampling different populations as well as from changes in the condition of resident individuals. On many estuaries in autumn and spring the presence of passage birds from populations other than the wintering population is well known. Population turnover during winter itself has also been found in species such as Knot (Dugan 1981a). Seasonal changes in population size during winter vary intraspecifically on different estuaries in species such as Grey Plover, Bar-tailed Godwit and Knot (Dugan 1981a). Patterns of fat and protein storage can be interpreted correctly only if there is detailed information on population turnover for each estuary from which condition samples were collected. This currently exists for few estuaries and species. A knowledge of population turnover is also important in identifying those samples in which the size of fat and protein reserves may have been depressed due to recent arrival.

Identification of known resident and transient individuals

Transient and resident individuals in a wintering population may have different seasonal patterns of nutritional condition. Known residents can be readily identified, if birds are marked early in the winter, as birds caught or seen twice on one estuary during the same winter. If known

residents have not been included in condition samples, their presence can be confirmed by comparison of the seasonal pattern of fat reserves with the total body weight changes of known resident individuals. I have used this technique for Sanderlings (Figure 26), Dunlins (Figure 28), Knots (Figure 25) and Grey Plovers (Figure 27).

The main difficulty is the identification of transient individuals in condition samples. The nutritional condition of transients could be affected by the fat and protein requirements of interestuarine movements in addition to the requirements for survival during severe weather. At present the only individuals that can be positively identified as transients would be those with a known history of movement within one winter, i.e. individuals marked on another estuary earlier in the winter. For most shorebirds there are very few individuals with a known history of within-winter movements even in species which are regularly caught on many estuaries. Intraspecifically, patterns of itinerancy can vary between individuals, as discussed for Knots moving between British estuaries by Dugan (1981a). Therefore individuals following several different patterns of interestuarine movement and so with different levels of fat and protein reserves could occur on one estuary at the same time. These are unlikely to be identified in a sample or population. To determine the seasonal changes in the nutritional condition of individual transients would require the sequential sampling of known transient populations on the series of estuaries visited by the population during one winter. Patterns of interestuarine movements are insufficiently documented for this to be feasible for most species as yet.

Many changes in lipid indices caused by interestuarine movements are probably detectable. For example, it can be calculated from Table 21 that Knots flying from the Wash to Teesmouth (a distance of 220 km.) in early December would have used about 5.5 g. of fat, equivalent to a change in lipid index of 3.5%. Although a difference of this magnitude would be too small to enable identification of all individual transients, some may be identified as carrying different fat reserves to a known resident population.

SUMMARY

The normal size of the fat and protein reserves of nine species of shorebirds are examined during the non-breeding seasons at two estuaries (Lindisfarne and Teesmouth) in north-east England, using laboratory analysis of carcasses and total body weights of live birds. Fat reserves are measured as a lipid index (fat as a percentage of total body weight), protein reserves as indices of pectoral muscle size. Changes in total body weight are mainly changes in the size of fat reserves. Fat reserves in resident wintering populations rise during autumn to a midwinter (December and/or January) peak and then decline until March. Protein reserves remain at a steady level throughout the winter. Before spring and autumn migrations fat is stored rapidly. Peak pre-migratory fat reserves are close to the theoretical maximum of 50% total body weight. Protein reserves increase only during spring.

Both fat and protein reserves are regulated during winter. The decline in fat reserves after midwinter results from the trade-off between decreasing probability of severe weather

occurring and the disadvantages of a large fat load. The size of the nutritional reserves maintained by each species depends on the extent of reductions in food intake, whether night feeding takes place, the extent of exposure to high windchills, and the extent of interestuarine movements during winter. Peak midwinter lipid indices are higher in plovers (> 20% total body weight) than estuarine sandpipers (12 - 15% total body weight), mainly as a consequence of the greater reductions in the food intake of plovers at low temperatures than those of shorebirds feeding by touch. Because of a continuously available food supply rocky shore species (e.g. Turnstone, Purple Sandpiper) store little fat. Itinerant species such as Knot tend to carry larger reserves than resident species.

As a consequence of their lower average feeding efficiency, first-year shorebirds regulate fat reserves at similar or higher midwinter levels than conspecific adults.

Factors leading to increased reserve storage involve morphology, feeding behaviour (e.g. visual feeding, field feeding) and migrations (e.g. cold weather movements, itinerancy). Shorebirds whose energy balance is most affected by high windchills (causing increased energy expenditure for thermo-regulation), gales (causing buffeting) and low temperatures (causing reduced prey activity and frozen substrates) store the largest nutritional reserves.

An understanding of population turnover, itinerancy and the presence of resident populations is essential in the interpretation of seasonal cycles of nutritional condition from periodic samples.

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Paper 2. Survival of shorebirds (Charadrii) during severe weather: the role of nutritional reserves

INTRODUCTION

During winter, shorebirds face increasing difficulty in achieving sufficient rates of prey intake to satisfy their energy requirements, as a result of the deterioration in environmental conditions. The effects of severe winter weather are twofold. Firstly, invertebrate prey species living in muddy or sandy substrates often become less available to shorebirds, either because they become less active and so less detectable, or by lying deeper in the substrate, mainly in response to low temperatures, but also to high winds (Smith 1975). These changes in prey availability, and the responses to them by shorebirds, are discussed by Evans (1976, 1979), Pienkowski (1980a, b, 1981) and Dugan (1981). The responses by shorebirds involve changes mainly in foraging behaviour and/or in prey species taken (Goss-Custard 1969, Smith 1975, Evans 1976, Pienkowski 1980a, 1981). The second, direct, effect of severe weather on shorebirds is to increase the energetic costs of thermoregulation during periods of low temperatures and high winds. Gales can also affect shorebirds directly by preventing them from feeding on their preferred feeding grounds (Evans 1976, Dugan et al. 1981).

Other than changes in food and feeding behaviour, the main adaptation by shorebirds for overwinter survival is the storage of nutritional reserves. The main energy reserve in shorebirds

(Evans & Smith 1975, Davidson 1979, Dugan et al. 1981, Paper 1), as in other birds (e.g. Ward 1969, Newton 1969, Ankney 1977), is fat. Muscle protein, particularly the pectoral muscles, is also used as a nutritional reserve (Kendall et al. 1973, Evans & Smith 1975, Ankney 1977, Paper 1). Lipid reserves are metabolised whenever the rate of food intake is insufficient to balance the rate of energy expenditure, whilst muscle protein is metabolised only when little or no feeding is possible, and is used primarily to provide amino-acids for protein synthesis rather than energy (Evans & Smith 1975), except in the last stages of starvation.

Normal seasonal changes in the nutritional condition of shorebirds in north-east England have been discussed in Paper 1. This paper discusses the role of lipid and protein reserves in the survival of shorebirds through severe winter weather. It examines four aspects of the role of nutritional condition:

1) the extent to which different species of shorebirds use their nutritional reserves during the same periods of severe weather,
2) the use of nutritional reserves by Redshanks during even mild winters,
3) the nutritional condition at which shorebirds die from starvation, and
4) recovery after severe loss of condition, measured in relation to starvation levels.

METHODS

Shorebirds have been collected at Teesmouth (54°35'N 1°35'W) and Lindisfarne (55°40'N 1°50'W) in north-east England since 1971, for studies of nutritional condition

(Evans & Smith 1975, Paper 1), diet (Smith 1975, Millard 1976, Evans et al. 1979) and heavy metal pollution (Evans & Ward in prep.). For Redshanks, samples collected during mild winters are examined; for other species only samples collected during severe weather are discussed in this paper. Methods of analysis for lipid and protein reserves, involving drying of carcasses in vacuum ovens, followed by the extraction of lipids using petroleum ether in a Soxhlet apparatus are described in detail by Evans & Smith (1975) and Paper 1. Lipid indices (i.e. lipid weight expressed as a percentage of total body weight) of live samples of birds netted at Teesmouth have been estimated from formulae relating wing-length and bill-length to lean weight (Appendix 2). Total body weights of Redshanks netted on estuaries throughout Britain are also examined.

Most published weights of shorebirds that had starved to death have been given as total body weight. For comparison with 'normal' winter lean weights, starvation weights have been reduced by 1% (Marcstrom & Mascher 1979, Davidson unpubl.), representing lipids unavailable for energy production (for example, in membranes).

Meteorological data have been obtained from several coastal weather stations close to Teesmouth and Lindisfarne and from elsewhere in Britain from the Meteorological Office (1976). Additionally, a windchill factor (W) has been calculated from the formula $W = TV^{\frac{1}{2}}$, where T is the mean daily temperature deficit below $20^{o}C$, and V is the mean daily windspeed in knots. This differs from the windchill factor calculated by Dugan et al. (1981), who used a temperature deficit below $10^{o}C$.

RESULTS

Loss of nutritional condition during severe weather

Information on the nutritional condition of several shorebird species was collected during two periods of severe winter weather: a brief spell during February 1978, and the prolonged severe weather of early 1979.

February 1978

Seven days of severe weather occurred between 9 February and 15 February. Pastures were snow-covered, daytime temperatures barely rose above 2^{o}C and on several days strong winds caused high windchills.

Samples of three shorebirds (Dunlins from Teesmouth, Bar-tailed Godwits and Golden Plovers from Lindisfarne) were collected with difficulty at the beginning and end of the period of severe weather and showed marked differences in the extent of mobilisation of their nutritional reserves. Weather conditions were similar in both areas, and there were no marked changes in the population sizes of Dunlins or Bar-tailed Godwits during this period. The 'before-' and 'after severe weather' samples of these two species are therefore thought to be from the same populations. Golden Plover population changes are discussed below.

Adult Dunlins used neither lipids nor protein during six days of severe weather (Table 1). However, first-year Dunlins had a lower mean lipid index after the severe weather (Table 1). This resulted from some individuals having lower lipid indices after the cold spell than any recorded before, whilst the highest lipid indices remained similar. Variability in lipid index after the cold spell was significantly greater

Table 1. Nutritional condition of Dunlins at Teesmouth at the beginning and end of a period of severe weather in February 1978

		Beginning (9 February)			End (15 February)			P
		n	$\bar{x} \pm 1$ s.e.	range	n	$\bar{x} \pm 1$ s.e.	range	(Student's t)
Adult	Lipid index (%)[a]	15	9.7 ± 0.7	5.5 - 13.8	4	9.9 ± 0.3	9.0 - 10.4	n.s.
	Pectoral Muscle Index[b] (SMV)	15	.281 ± .005	.258 - .330	4	.272 ± .012	.242 - .299	n.s.
	Pectoral Muscle Index[c] (% LW)	15	5.75 ± 0.07	5.24 - 6.32	4	5.88 ± 0.16	5.58 - 6.31	n.s.
	Lean Weight (g.)	15	48.3 ± 1.0	43.1 - 54.7	4	47.2 ± 0.7	46.1 - 48.8	n.s.
First-year	Lipid Index (%)	11	8.5 ± 0.6	5.3 - 11.2	6	7.8 ± 1.4	3.5 - 11.9	n.s.
	Pectoral Muscle Index (SMV)	11	.281 ± .007	.239 - .309	6	.279 ± .011	.255 - .321	n.s.
	Pectoral Muscle Index (% LW)	11	5.77 ± 0.10	5.06 - 6.27	6	5.98 ± 0.10	5.76 - 6.42	n.s.
	Lean Weight (g.)	11	47.6 ± 1.1	41.3 - 51.2	6	46.6 ± 1.1	44.0 - 48.6	n.s.

a Lipid Index = $\frac{\text{fat}}{\text{total body wt. (g.)}} \times 100$

b Pectoral Muscle Index (SMV) = $\frac{\text{lean dry pectoral muscle (g.)}}{\text{standard muscle volume}}$ (for details of method see Paper 1).

c Pectoral Muscle Index (% LW) = $\frac{\text{lean dry pectoral muscle (g.)}}{\text{lean weight (g.)}} \times 200$

in first-years than adults (First-yr./Adult, $F_{5,3} = 31.75$ $P < .01$), as would be expected if some first-years but no adults had catabolised fat reserves. Protein reserves were not used by first-year Dunlins during the severe weather.

In Bar-tailed Godwits (Table 2) the lower lipid and protein levels on 15 February are consistent with the use of some nutrient reserves, but sample sizes are small and none of the differences are significant.

In contrast to Godwits and Dunlins, Golden Plovers drew extensively on their nutrient reserves during the same period, both lipid and muscle protein levels decreasing significantly (Table 3). This extensive use of nutrient reserves was a result of heavy snowfall at the start of the cold period making pastures, the preferred habitat of Golden Plovers (Fuller & Youngman 1979), unusable . Numbers of Golden Plovers on Lindisfarne decreased early in the severe weather (pers. obs., J. Brigham pers. comm.). Birds possibly moved south or south-west, as recorded during previous severe weather by Ash (1964) and Dobinson & Richards (1964). Although the sample taken at the end of the severe weather may therefore be representative of only part of the population present at the start of the cold spell, the Golden Plovers collected on the 14 February had undoubtedly mobilised nutrient reserves during the severe weather since the ranges of values were non-overlapping (Table 3). All birds in the 8 February sample (i.e. at the start of the severe weather) were carrying very similar lipid levels. Those Golden Plovers that remained on Lindisfarne moved to the intertidal mudflats where they were subjected to interspecific aggression, particularly from Grey Plovers (pers. obs., D.J. Townshend pers. comm.),

Table 2. Nutritional condition of adult Bar-tailed Godwits at Lindisfarne at the beginning and end of a period of severe weather in February 1978, indices calculated as Table 1. Lean weights are omitted because of the large variations in body size of this species (Evans & Smith 1975).

	Beginning (9 February)			End (15 February)			P
	n	$\bar{x} \pm 1$ s.e.	range	n	$\bar{x} \pm 1$ s.e.	range	(Student's t)
Lipid Index (%)	3	11.3 ± 3.9	5.7 - 18.7	2	8.7 ± 2.0	6.6 - 10.7	n.s.
Pectoral muscle index (SMV)	3	.278 ± .024	.240 - .322	2	.255 ± .027	.227 - .282	n.s.
Pectoral muscle index (% LW)	3	6.19 ± 0.05	6.13 - 6.29	2	5.96 ± 0.46	5.52 - 6.43	n.s.

Table 3. Nutritional condition of adult Golden Plovers at Lindisfarne at the beginning and end of a period of severe weather in February 1978.

	Beginning (8 February)			End (14 February)			P
	n	$\bar{x} \pm 1$ s.e.	range	n	$\bar{x} \pm 1$ s.e.	range	(Student's t)
Lipid Index (%)	10	24.2 ± 0.8	18.5 - 26.6	2	7.7 ± 2.1	5.6 - 9.8	<.001
Pectoral Muscle Index (SMV)	10	.323 ± .008	.281 - .356	2	.244 ± .023	.217 - .272	<.010
Pectoral Muscle Index (% LW)	10	7.75 ± 0.14	7.08 - 8.51	2	6.45 ± 0.48	5.97 - 6.93	<.050
Lean Weight (g.)	10	180.4 ± 5.4	149.3 - 213.3	2	163.6 ± 5.1	158.5 - 168.8	<.050

as well as encountering the same severe weather conditions as intertidal shorebirds.

January - March 1979

The 1978/79 winter was the most severe for 16 years. The worst conditions occurred between late December 1978 - mid January 1979, and again in mid February 1979. No carcasses were analysed, but sufficient live samples of Dunlin and Grey Plover were netted at Teesmouth to make estimates of lipid indices, using formulae from Appendix 2.

Grey Plover

Dugan et al. (1981) document the normal seasonal changes in total body weight and those in winter 1978/79. The only sample with weights significantly below normal was netted on 12 January, when six birds averaged 137 g. Since normal lean weights in winter average 210 g. (Paper 3), these birds must have metabolised all their available lipid reserves and they had, in addition, lost up to 35% of their normal lean weight. Despite this extensive use of lipids and muscle protein, most of these birds are known to have survived, and to have regained their normal total body weights by the end of February.

Lipid index estimates, calculated from total live weights, (Figure 1), suggest that the Teesmouth population of Grey Plovers had not regained all their lipid reserves by the end of January (i.e. two weeks later). However, this apparently low lipid index could also have been obtained from the low live weight if lipid levels had returned to normal, but lean weight was still below normal (i.e. if the lean weight calculated from the formula in Appendix 2 was an overestimate). It is not clear which of these two alternatives occurred.

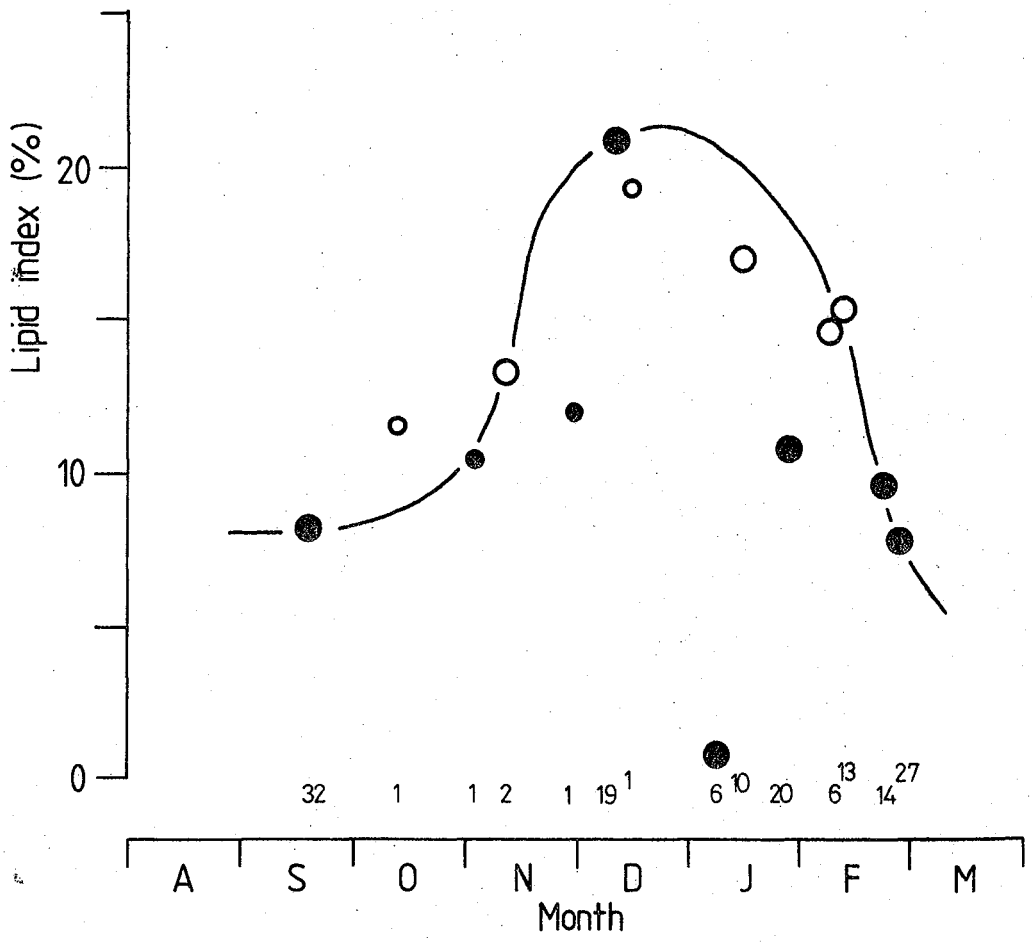


Figure 1: Mean lipid indices estimated from the total body weights of Grey Plovers at Teesmouth, during the 1978/79 winter (●), and other years (O). Numbers indicate sample sizes; trend line fitted by eye.

Captive Mallard, Anas platyrhynchos that had been starved, regained 80% of their total weight within a week of unrestricted food being made available (Jordan 1953). Dugan et al. (1981) attributed the poor nutritional condition of Grey Plover on 12 January primarily to periods of gales, and documented that this species cannot feed successfully on open mudflats at Teesmouth when the windspeed exceeds 25 knots.

Dunlin

Lipid indices estimated from live birds caught during January and February 1979 were consistently lower than during the less severe weather of January and February 1980 (Figure 2). There were two periods in early 1979 when lipid reserves appear to have been used extensively: early January and late February. These coincided with the two periods of most severe weather. In late December 1978 and early January 1979 windchill was consistently high, with consecutive days when windchill was above 85. Conditions improved in late January and early February, and Figure 2 shows that by early February both adult and first-year Dunlin had regained some of the lipid reserves that had been previously mobilised. During mid February, the second period of marked lipid index decline, there was a period when windchill was above 100 on five consecutive days. Weight losses of individual Dunlins followed a similar pattern to those of the population in January and February 1979 (Paper 1: Figure 28).

First-year Dunlins had higher lipid indices than adults during January and February in the mild conditions of 1980 (Figure 2), but the lipid indices of first-years declined more rapidly during this period as found from carcass analysis

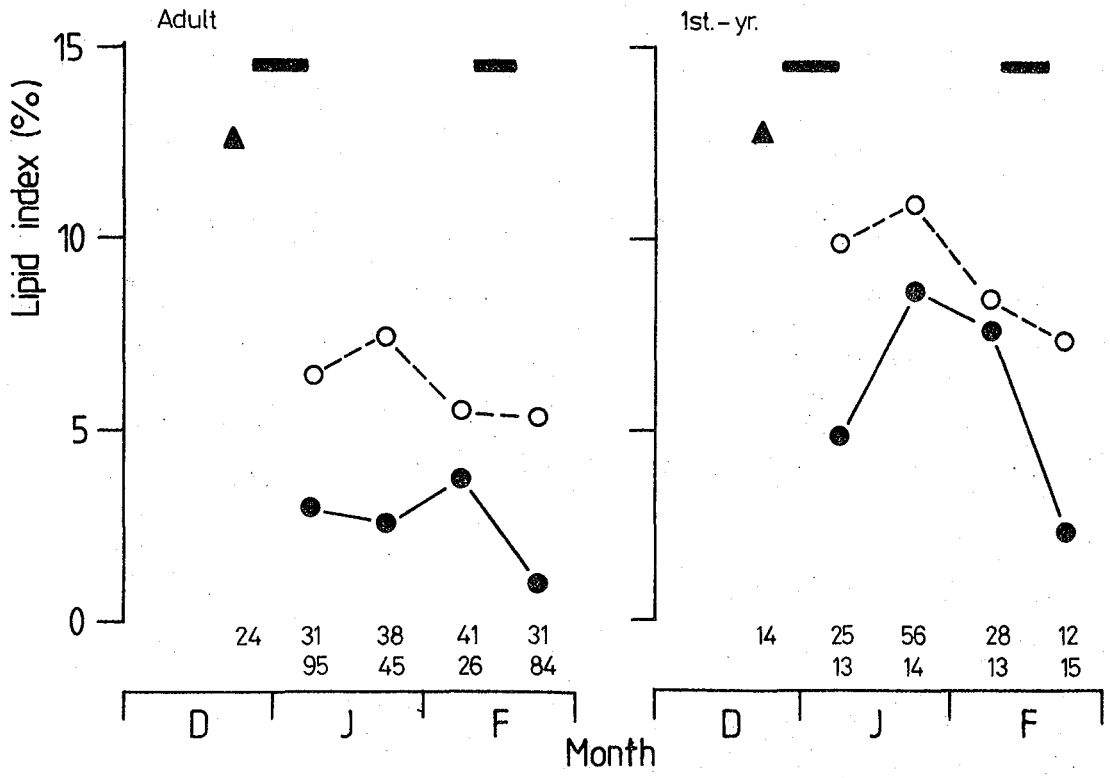


Figure 2: Mean lipid indices estimated from the total body weights of adult and first-year Dunlins at Teesmouth during the severe weather in Jan./Feb. 1979 (—●—) and during a mild winter (Jan./Feb. 1980) (--o--). Late December 1975 values (▲) are also shown. Numbers indicate sample sizes. Horizontal bars indicate the periods of most severe weather in 1979.

in previous winters (Paper 1). During the two periods of severe weather in early 1979, first-years metabolised on average more lipids than adults: in early January, lipid indices were 3.5% lower in adults and 5% in first-years in 1979 than in 1980; in mid February the differences were 4.3% in adults and 5.1% in first-years. This is consistent with the prediction (Paper 1) that first-year shorebirds, because of their poorer feeding efficiency, are less able to maintain regulated levels of fat reserves.

The low calculated lipid indices during the two periods of severe weather in early 1979 could be underestimates if loss of lean weight as well as lipids had occurred. However, for reasons discussed by Evans & Smith (1975), if muscle protein was being metabolised during these periods of severe weather, then lipids reserves were undoubtedly also being used. The conclusion that nutritional reserves were being used therefore remains valid, but the declines in lipid reserves may be overestimates. Another possible explanation of the low lipid levels in early 1979 could be that neither adult nor first-year Dunlins had managed to attain their normal peak lipid indices (above 15%) in late December 1978. Unfortunately, very few Dunlins were caught during this period, but an average lipid index of over 7% in a sample of first-years in early November conforms to the normal lipid index pattern during mild weather (Paper 1). Adherence to the normal pattern by adults in late 1978 is more difficult to demonstrate since few birds known to have stayed at Teesmouth throughout the autumn were caught in December.

The greater use of nutritional reserves during severe winter weather by plovers than sandpipers correlates with

the higher regulated lipid levels and larger pectoral muscles of plovers (Paper 1). This supports the suggestion (Evans & Smith 1975, Pienkowski, Lloyd & Minton 1979) that winter lipid levels are a trade-off between the need to carry sufficient nutritional reserves for survival through periods of severe weather and the disadvantages, probably energetic and aerodynamic, of carrying an increased weight-load of lipids during non-migratory periods (Dick & Pienkowski 1979, Pienkowski, Lloyd & Minton 1979, Paper 1).

Loss of nutritional condition by Redshanks during winter

20 Redshanks were collected at Teesmouth and 17 at Lindisfarne during the winters of 1971/72 and 1972/73, but as there were no detectable differences in body composition of birds from the two areas, data from both have been combined. Redshanks were not collected during more recent winters, most of which have been more severe than 1971/72 and 1972/73. Problems exist in the ageing of Redshanks after midwinter using plumage characteristics (W.G. Hale, pers. comm.), and so data for all age-groups have been combined.

Fat Reserves

From the small samples, it appears that the mean lipid index of Redshanks in November (12.3%) was higher than in October or December (Figure 3). After November, lipid indices were very low, averaging only 3.6% in January and 2% at the end of February. Between November and February, lipid indices were negatively correlated with date (Spearman $r_{17} = -.576$ $P < .05$). By late March, lipid indices were significantly higher than at the end of February ($\bar{x}$ February 2.06%(6), late March 10.20%(6), $t_{10} = 4.53$ $P < .01$), and during this period were correlated with date (Spearman $r_{18} = .671$ $P < .01$).

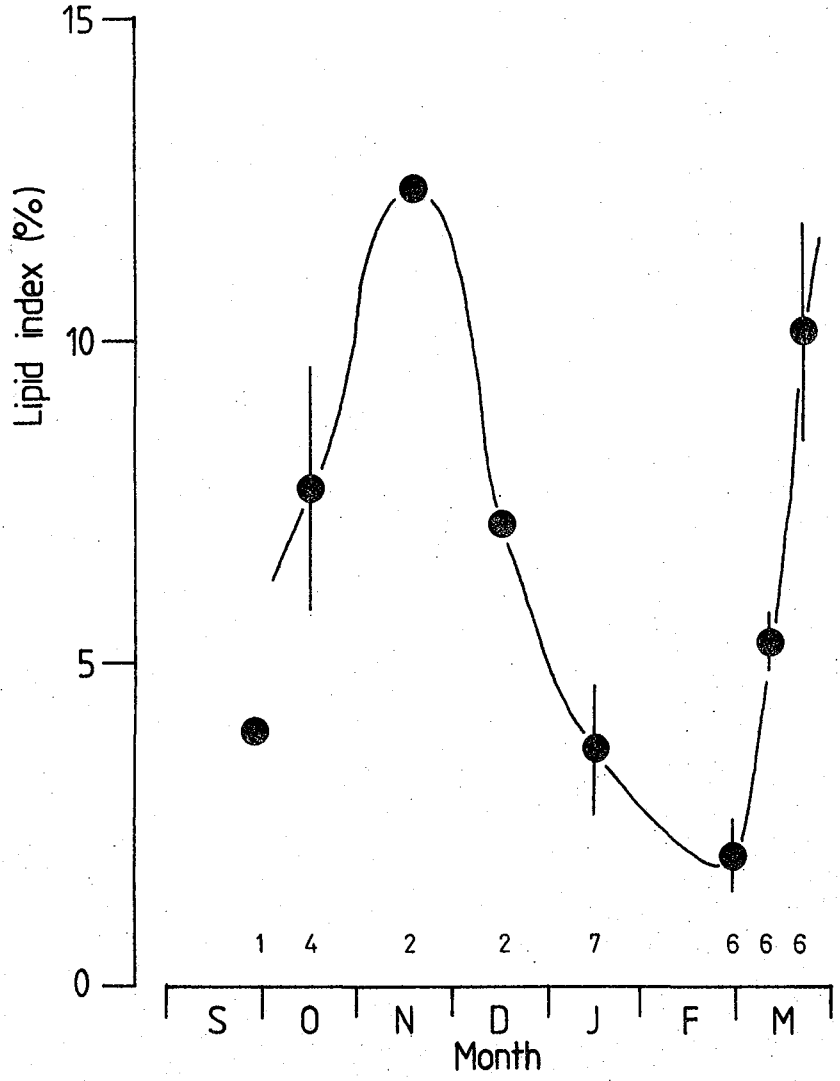


Figure 3: Lipid indices of Redshanks in north-east England during 1971/72 and 1972/73. Each point is the mean ± 1 standard error. Numbers indicate sample sizes. trend line fitted by eye.

Although the decrease in lipid index occurring between November and December could be due to the inclusion of passage birds (with high lipid indices for further migration) in November, by late February the lipid indices carried by Redshanks at Teesmouth and Lindisfarne were significantly lower than in all other shorebirds (Table 4). The late February mean lipid index of 2% indicates that Redshanks carried very little non-structural fat reserve at that time of year, and all birds collected were in very similar condition, the highest lipid index recorded being only 4.1%.

Pectoral Muscle Size

In north-east England, pectoral muscle size as a proportion of SMV remained unchanged between September and November, averaging .26 - .28 SMV, but by late February pectoral muscle sizes were much lower, averaging only .175 SMV (Figure 4a). Between November and February, pectoral muscle size was negatively correlated with date (Spearman $r_{16} = -.605$ $P < .05$). Redshanks had significantly smaller pectoral muscles than all other shorebirds in late February (Table 5). They were the only shorebird species in north-east England in which pectoral muscle indices became smaller as the winter progressed: in other species pectoral muscle size is steady throughout the winter (Paper 1). Pectoral muscle size in March ($\bar{x}$ .24 SMV) was more variable but larger than in February and approached that of early winter.

Pectoral muscle size as a percentage of total lean weight (Figure 4b) changed seasonally in a similar way to the SMV index, being lower in February (4%) than in early winter (5%), and returning to the early winter level by March (5.25%). The difference between February and March was significant ($t_{16} = 3.00$ $P < .02$).

Table 4. Lipid Indices of Redshanks in comparison with other shorebirds between early February and early March in North-East England

	Date	Lipid Index (%)	Significance of difference from Redshank (Student's t)
Redshank	26/28 Feb.	2.06 ± 0.55 (6)	
Dunlin	12 Feb.	10.16 ± 0.66 (18)	< .001
	15 Feb.	9.90 ± 0.30 (4)	< .001
	26 Feb.	7.05 ± 0.83 (2)	< .005
Knot	9 Feb.	13.16 ± 0.79 (9)	< .001
	7 Mar.	11.48 ± 0.74 (5)	< .001
Bar-tailed Godwit	9 Feb.	11.29 ± 2.86 (3)	< .050
	4 Mar.	10.39 ± 1.94 (3)	< .005
Sanderling	5 Feb.	20.89 ± 5.48 (2)	< .020
	8 Mar.	7.63 (1)	

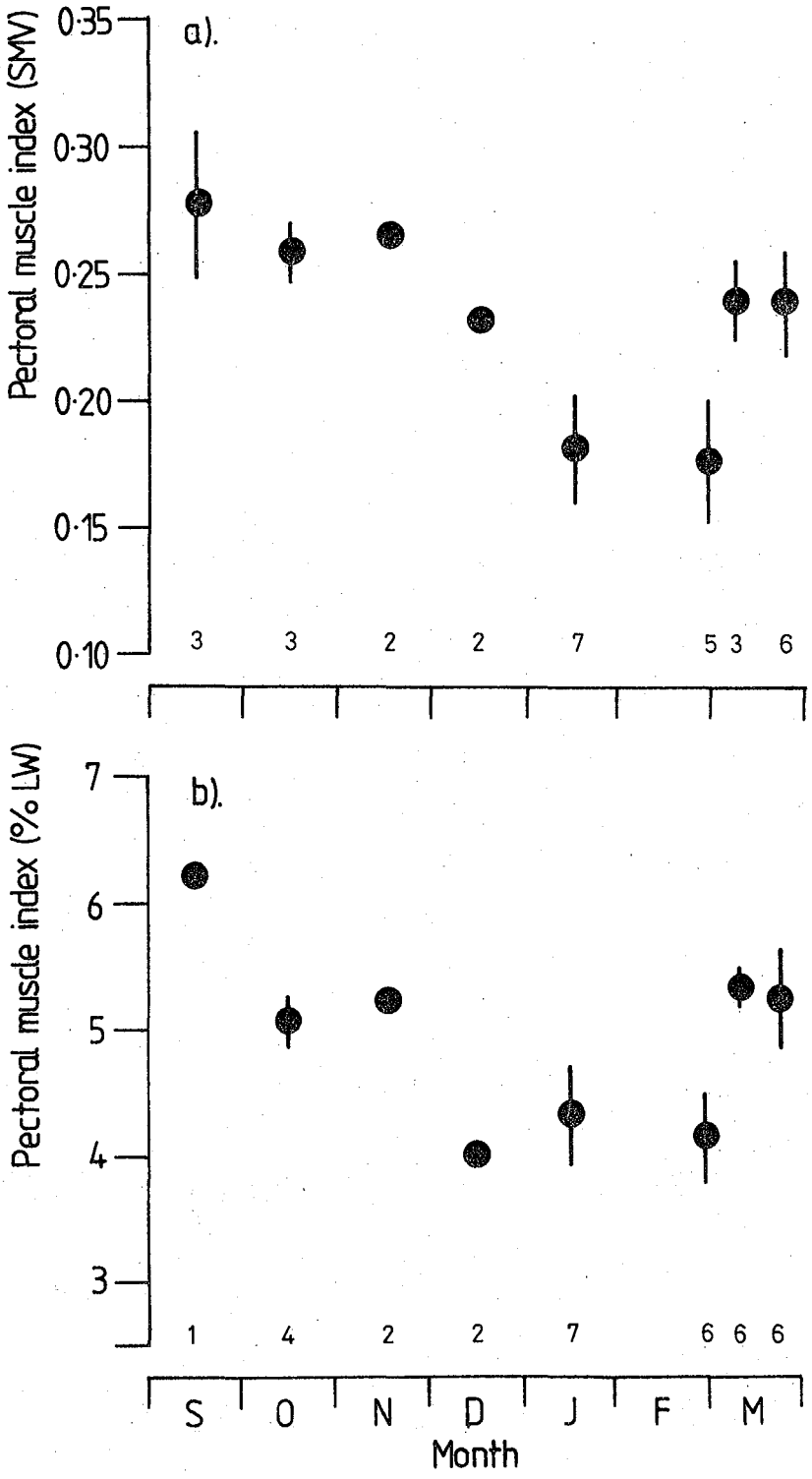


Figure 4: Pectoral muscle indices of Redshanks in north-east England during 1971/72 and 1972/73, a) as a proportion of the standard muscle volume, and b) as a percentage of lean weight. Each point is the mean ± 1 standard error. Numbers indicate sample sizes.

Table 5. Pectoral muscle size (as a proportion of a standard muscle volume) in Redshanks compared with other adult shorebirds during late winter

Species	Date	Pectoral Muscle Size	Significance of difference from Redshank (Student's t)
Redshank	26/28 Feb.	.176 ± 0.24 (5)	
Dunlin	12 Feb.	.270 ± .007 (16)	< .020
	15 Feb.	.272 ± .012 (4)	< .010
	26 Feb.	.226 ± .010 (2)	n.s.
Knot	9 Feb.	.303 ± .009 (9)	< .002
	7 Mar.	.311 ± .007 (5)	< .002
Bar-tailed Godwit	9 Feb.	.278 ± .024 (3)	n.s.
	4 Mar.	.304 ± .006 (3)	< .020
Sanderling	5 Feb.	.282 ± .031 (2)	n.s.
	8 Mar.	.284 (1)	

Total Lean Weight

Total lean weights of Redshanks in north-east England (Figure 5), like lipid and pectoral muscle indices, were negatively correlated with date from November to January (Spearman $r_{11} = -.561$ $P < .05$). Total lean weight remained low during February but was significantly higher in late March ($\bar{x}$ February 117.5 g. (6), Late March 140.5 g. (6), $t_{10} = 2.94$ $P < .05$). Between November and February the change in total lean weight (21.6%) was less than in pectoral muscle size (33.4%) suggesting, if the samples were representative of the same population, that pectoral muscle tissue was mobilised more extensively than other components of lean weight.

A marked decline in the condition of some birds known to be resident also occurred on the Firth of Forth in 1979/80, another mild winter. Total body weights of individuals weighed at least twice during the 1979/80 winter are shown in Figure 6. (Changes in total body weight reflect changes chiefly in the weight of fat - Paper 1). One might have expected individual Reshanks to have increased in weight between October and January since the mean weight of all birds was 12 g. higher on 13 January 1980 than on 30 October 1979. However, of 34 adult Redshanks weighed on both dates, 11 (32%) either had not changed or had lost weight. Both first-year Redshanks weighed on both dates also lost weight. Maximum weight losses were 10% in adults and 8% in first-years. Variability in weight of the recaptured adult Redshanks was significantly greater in January than in October (13 Jan. 1980/30 Oct. 1979, $F_{33,33} = 2.27$ $P < .05$). All nine adults weighed first in mid-January and then again in February or March lost weight, the

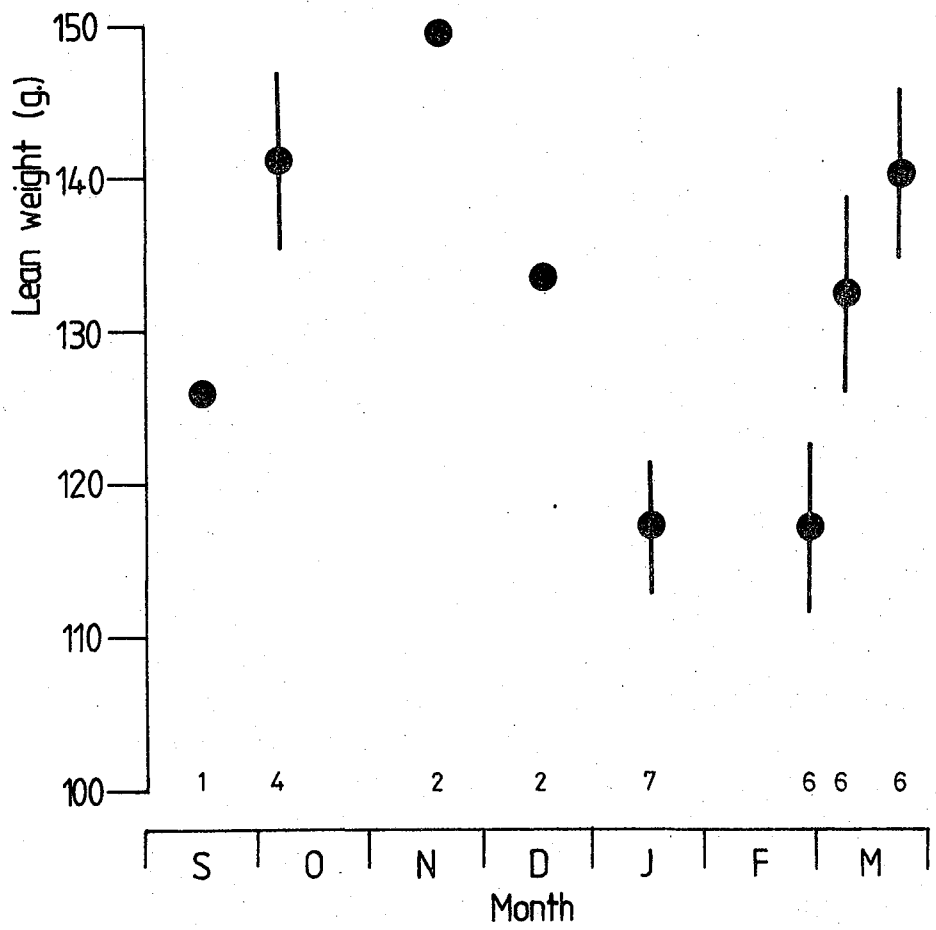


Figure 5: Lean weights of Redshanks in north-east England during 1971/72 and 1972/73. Each point is the mean ± 1 standard error. Numbers indicate sample sizes.

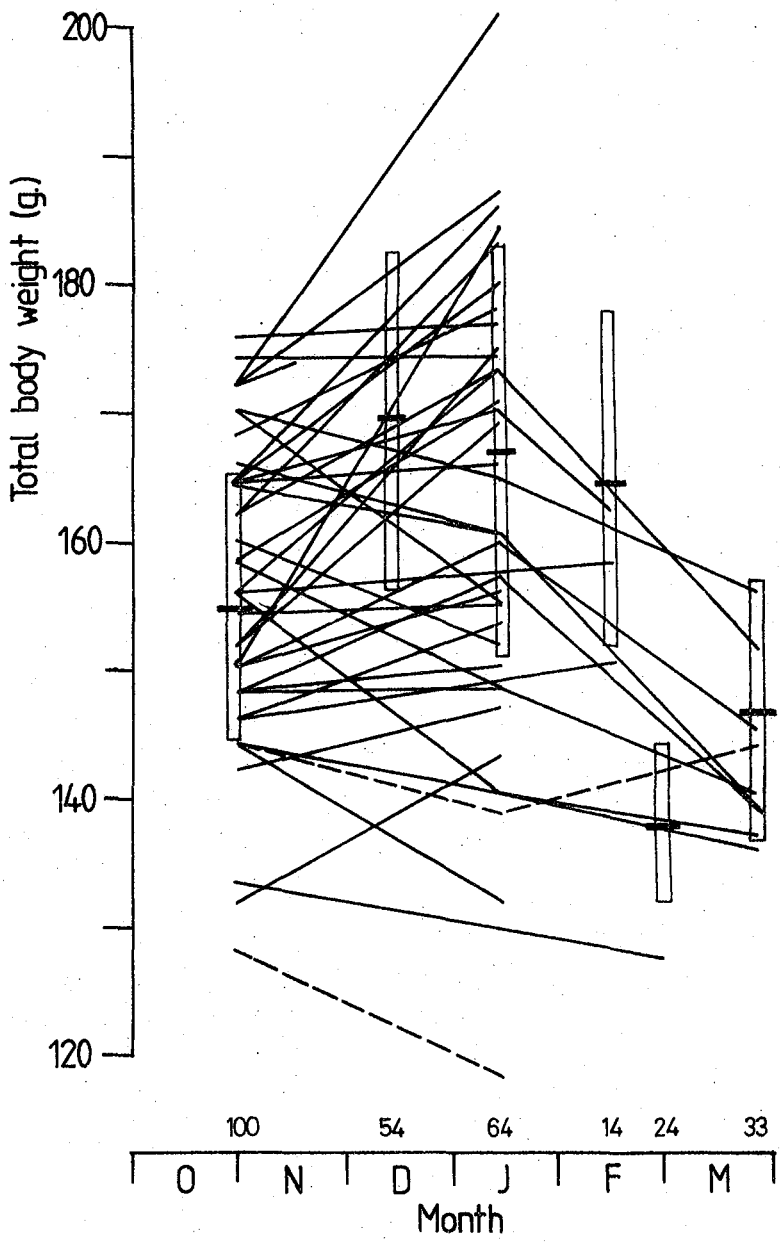


Figure 6: Total body weight changes of Redshanks caught more than once on the Firth of Forth during the 1979/80 winter. Solid lines join weights of each adult and dashed lines join weights of each first-year. For clarity, 20 adults and 6 first-years caught in October and March only are omitted. Open boxes show the mean $\pm$ 1 standard deviation of all adult Redshanks weighed during the 1979/80 winter. Numbers indicate sample sizes.

maximum loss being 14% of total body weight. The mean weight of Redshanks on 29 February 1980 was 10 g. below the normal early winter lean weight, implying that Redshanks on the Forth, as at Teesmouth,carried very low fat reserves by late February, and that some losses of lean body weight may have also occurred.

Neither on the Forth, the Wash nor at Teesmouth was there a marked midwinter peak in the total body weight of live Redshanks (Figure 7a). Total body weight decreased rapidly in February on the Wash, as on the Forth, but this cannot be confirmed for Teesmouth because no Redshanks have been caught there in late February. Total body weights followed similar seasonal patterns and levels on each estuary. Rapid decreases in total body weight are not confined to Britain: on the Dutch Waddensee similar declines in total body weight after December to those on British east coast estuaries occurred in both Continental and Icelandic Redshanks (Figure 7b).

Seasonal changes in water content could not be examined because original total body weights were not recorded for most of the specimens analysed for body condition.

Nutritional condition at death from starvation

Reserves of lipids and protein are not always sufficient to ensure survival in exceptionally severe weather, and individuals of many shorebird species have then been recorded as having starved to death. In cases where fat and protein levels have been analysed, lipid reserves have been exhausted at death, since the lipid indices of less than 1.5% recorded (Marcstrom & Mascher 1979, pers. obs.) are probably structural lipids. In passerines, very similar structural lipid levels have been recorded in the tropical bulbul *Pycnonotus goiavier* (Ward 1969) and the Bullfinch *Pyrrhula pyrrhula* (Newton 1969).

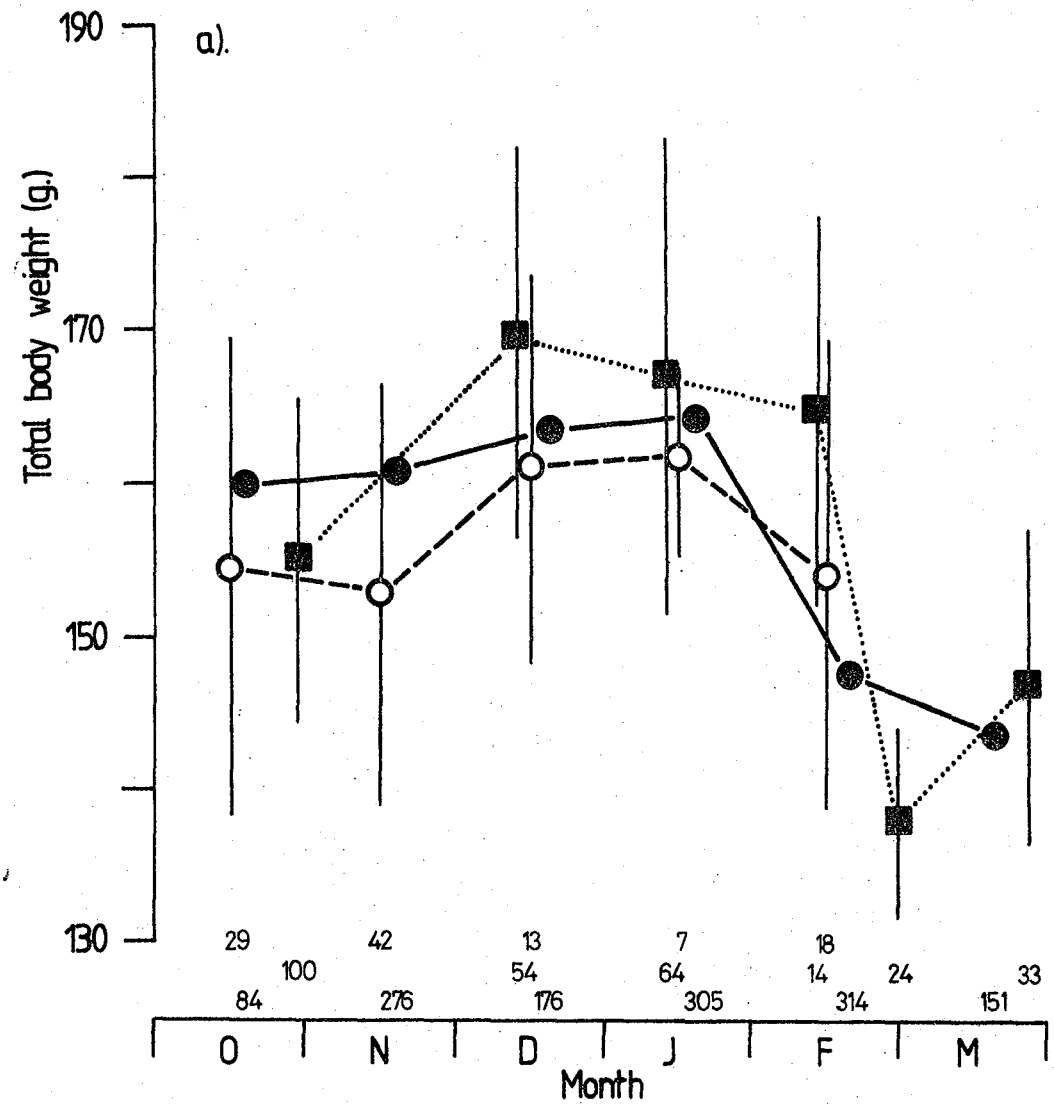
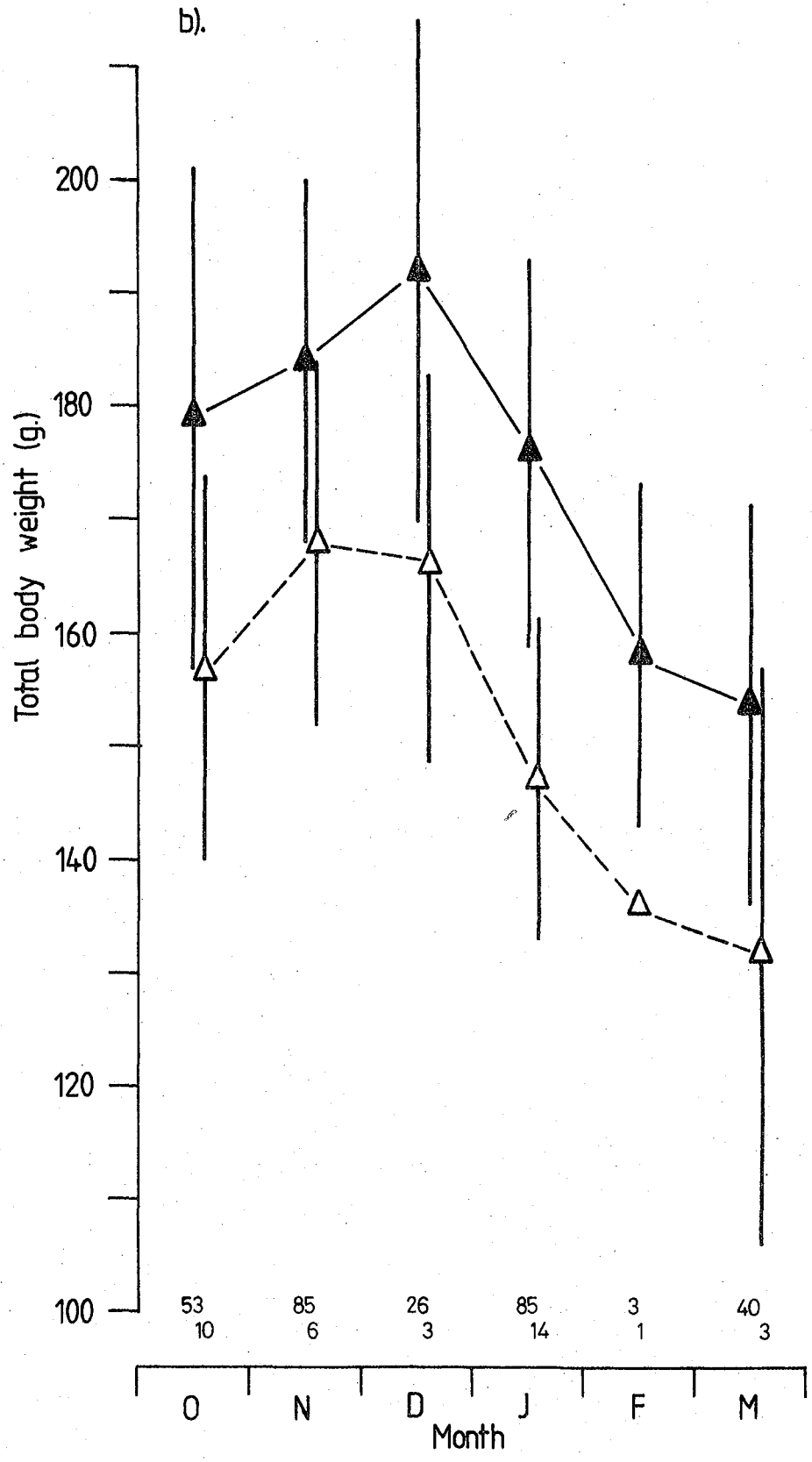


Figure 7: Total body weights of adult Redshanks wintering on various estuaries. a) on the Wash (—●—) from Branson (1979), on the Firth of Forth in 1979/80 (·····■·····) and at Teesmouth (---○---). Weights from the Wash and Teesmouth are grouped by month; weights from the Forth are plotted on date of capture, and b) presumed Icelandic (—▲—) and Continental (---Δ---) Redshanks on the Dutch Waddensee, from Smit and Wolff (1981). Each point is the mean ± 1 standard deviation. Means only are shown for the Wash. Numbers indicate sample sizes.


b).
Total body weight (g.)
200
180
160
140
120
100
53
10
85
6
26
3
85
14
3
1
40
3
O
N
D
J
F
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Month

Figure 7b.

In addition, muscle protein has been extensively utilised by the time death occurs, resulting in a marked drop in lean weight. Comparison of death weights with 'normal' total body weight is unsatisfactory, as indicated by Marcstrom & Mascher (1979), because large seasonal variations in the size of the lipid reserves mean that the 'normal' weight also changes markedly from month to month. (Lean weights also vary seasonally (Paper 3), but the variations are much smaller.) In the following discussion inter- and intraspecific comparisons of nutritional condition at death are made by examining losses only in lean weight (below normal winter lean weight levels). Water content decreases in proportion to lean weight (Marcstrom & Mascher 1979) and so, although about two-thirds of a lean weight loss is a loss of water, the conclusions on the use of protein remain valid.

Lean weight losses at death (Table 6) varied between 21% and 42%, averaging about 30%. There is considerable variation in the extent of the lean weight loss at death within a single species. There is, however, a constant relationship between the lean weight level at death and body size (wing-length) during the same period of severe weather in one area (Figure 8). Similar relationships exist for normal lean weights in coastal shorebirds (Paper 3), but the slope of the regression for birds that had starved to death is significantly less than that for birds in normal condition during winter ($t_{13} = 3.14$ $P < .01$). Small species of shorebirds apparently lose proportionally less lean weight at death that large species, possibly because small species have higher metabolic rates per unit weight (Kendeigh, Dol'nik & Gavrilov 1977). Shorebirds that do not use inter-tidal feeding areas extensively during the non-breeding season

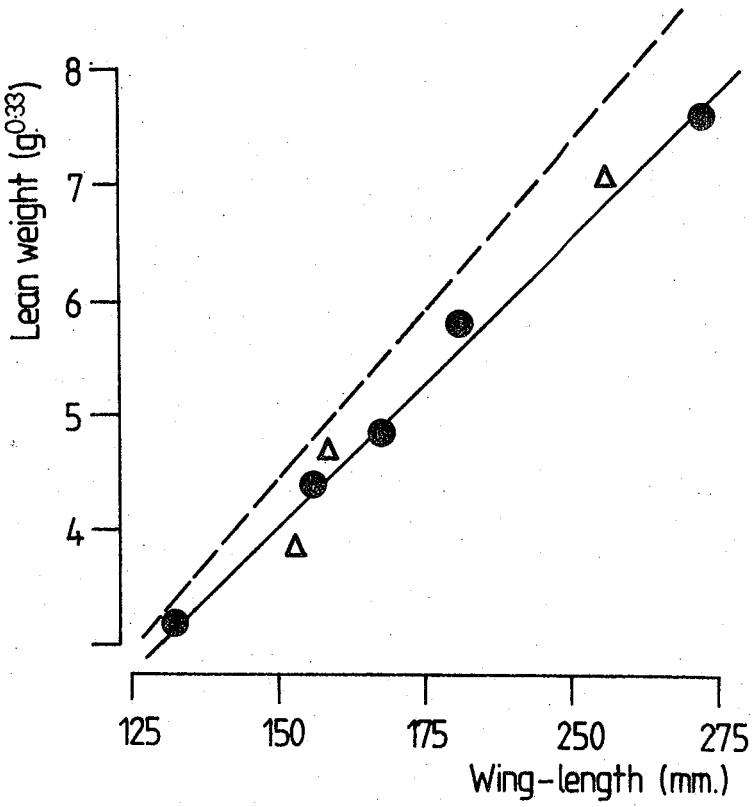

Figure 8 : The relationship between lean weight and wing-length in shorebirds that had starved to death during severe weather, from Ash (1964) (●), and from other sources (Δ). The least squares regression (——), calculated on species from Ash (1964) only, is Lean Weight$^{0.33}$ = .0247 Wing-length + .3881, r_3 = .9974, P < .001. The dashed line shows the regression for adult coastal shorebirds in normal winter condition in north-east England, from Paper 3.

do not conform to the same relationship of lean weight at death and body size, for reasons discussed in Paper 3.

Death from starvation during severe weather occurs most frequently in winter, but can also occur after shorebirds have arrived on their breeding grounds in spring, during periods of heavy snowfall and low temperatures (Vepsalainen 1968, Morrison 1975, Marcstrom & Mascher 1979). Because lean weights are higher in spring than in winter (Paper 1, Paper 3), the absolute amount of lean weight lost during these spring cold spells must be greater than that indicated in Table 6.

Differences in the percentage of lean weight lost at death are likely to be correlated with the severity of the weather conditions. When feeding is impossible, both lipids (as the main energy source) and muscle protein (as a source of amino-acids) are metabolised (Evans & Smith 1975). Once lipid reserves are exhausted, muscle protein must provide the energetic requirements as well. However, protein probably cannot be metabolised sufficiently fast when the energetic requirements are very high. Thus birds may die at higher lean weights during a brief, but very severe, period than during a prolonged but less severe cold spell. In agreement with this, in captive Mallard Jordan (1953) recorded the smallest total weight loss at death in birds starved during the winter, and the largest in summer, despite the fact that Mallard carry more fat in winter than summer (Owen & Cook 1977).

The shorebirds that are most susceptible to death by starvation fall into two categories: firstly, inland species, particularly Lapwing (Harris 1962, Dobinson & Richards 1964, Marcstrom & Mascher 1979) and, secondly, two coastal species, Redshank and Oystercatcher (Dobinson & Richards 1964, Goss-Custard et al. 1977, Marcstrom & Mascher 1979, Baillie 1980). High

Table 6. Lean weight losses in shorebirds that had starved to death during severe weather

	Source[a]	Lean wt. at death (g.)[b]	Normal winter lean wt. (g.)[c]	% loss[d]
Redshank *Tringa totanus*	1	84.4	130.8	35.5
	2	106.1*	139.0	23.7
Oystercatcher *Haematopus ostralegus*	2	357.4*	467.4	23.5
	3	304.0*	385.8	21.2
Black-tailed Godwit *Limosa limosa*	1	194.4	247.8	21.6
Curlew *Numenius arquata*	1	439.9	663.3	33.7
Dunlin *Calidris alpina*	1	32.6	46.9	30.5
Turnstone *Arenaria interpres*	4	58.8	101.3	41.9
Golden Plover *Pluvialis apricaria*	1	113.8	170.8	33.4
	5	112.9		(33.9)
Lapwing *Vanellus vanellus*	3	137.9*	201.3	31.5
	1	132.4		(34.3)
	5	132.9		(34.0)
	6	134.1		(33.4)
	7	121.1		(39.9)
Woodcock *Scolopax rusticola*	1	193.8	?	?

a. 1 Ash (1964) Poole Harbour, Sussex, Jan/Feb. 1963; 2 Davidson (unpubl.), Ythan, N.E. Scotland, Jan/Feb. 1979; 3 Marcstrom & Mascher (1979) South Sweden, April 1966; 4 Morrison (1975) Ellesmere Is., Canada, June 1974; 5 Harris (1962) Skomer Is., Wales, Jan. 1962; 6 Vepsalainen (1968) Finland, Spring 1966; 7 Creutz & Piechocki (1970) E. Germany.

b. Published lean weights are indicated by *. Other lean weights were estimated by total body weight - 1% lipids.

c. Except for Redshank from Davidson (unpubl.), weights were calculated from formulae in Paper 3.

d. Values in parentheses were calculated from normal winter lean weights from different sources.

winter mortality of Oystercatchers is largely of first-years (Heppleston 1971, Baillie 1980) whose weights decline rapidly between December and April on both the east and west coasts of Britain, whereas adults, unusually, gain weight gradually throughout the winter (Dare 1977, Branson & Minton 1978) as an adaptation for an early breeding season. No carcass analyses have been made on Oystercatchers, so the existence of low late winter fat reserves and a decline in pectoral muscle size in first-years during mild winters, similar to that of Redshank, cannot be investigated.

Recovery from severe loss of condition

Lipids can be mobilised and replaced rapidly, and temporary loss of all reserve lipids probably does not affect subsequent shorebird survival, since Redshank lose almost all their lipid reserves by the end of February even in mild winters Figure 3). Lipids can also become severely depleted during long non-stop migratory flights (e.g. Dick & Pienkowski 1979). However, after depletion on migration or during severe weather (Dugan et al. 1981) they can be replaced rapidly. Additional lipid reserves can also be accumulated rapidly in advance of migration (e.g. Pienkowski, Lloyd & Minton 1979, Summers & Waltner 1979, Paper 1).

Reductions in muscle protein weights may occur during migration as well as winter starvation(Evans & Smith 1975, Dick & Pienkowski 1979). Depletions during winter (examined as lean weight) that did not result in death are listed in Table 7. Losses by both Redshank during mild winters, and Golden Plover during severe weather in February 1978 are much less than the losses at which death has been recorded (21 - 42%).

In contrast, the loss of 35% lean weight by Grey Plover during January 1979 is more than the losses at death under many circumstances, although, because the pectoral muscles are larger in plovers than in other shorebirds, plovers can probably utilise a greater percentage of their lean weight than sandpipers before dying. These Grey Plovers had recovered to near their normal condition a fortnight after having severely depleted reserves. The level of lean weight from which recovery is possible must be very close to that at which death occurs, but this minimum recovery weight varies depending on species and severity of weather.

Table 7. Lean weight losses recorded in live shorebirds in north-east England during severe winter weather.

Species	Date	Lean wt. during severe weather(g.)	Normal winter lean wt. (g.)	% loss
Redshank	Jan/Feb 1972/73	117.2	139.0	15.6
Golden Plover	Feb 1978	163.6	180.4	9.3
Grey Plover	Jan 1979	135.6*	209.8	35.4

* estimated from total body weight - 1% lipids. Total body weight from Dugan et al. (1981).

DISCUSSION

The importance of nutritional reserves during severe weather

Plovers (Charadriidae) carry larger regulated fat and protein reserves than sandpipers (Scolopacidae) during winter in north east England (Paper 1). The differences in the catabolism of reserves I have documented in this paper show that plovers need to store larger reserves because they draw on their reserves during severe weather to a greater extent than do sandpipers. This plover/sandpiper difference arises mainly because plovers feed visually but sandpipers can feed also by touch. During severe weather, most invertebrate prey becomes inactive and remains below the substrate surface (Evans 1979, Pienkowski 1980a, b). As a consequence, plovers have greater reductions in food intake than sandpipers since inactive prey below the surface is still available to sandpipers (Pienkowski 1980a).

First-year shorebirds store the same or larger fat reserves than conspecific adults (Paper 1). The poorer average feeding efficiency of first-year than adult shorebirds (Paper 1) leads to the prediction that first-years store larger reserves because they must catabolise more fat than must adults during severe weather. Changes in the condition of Dunlins at Tees-mouth in 1978 and 1979 confirm this: when both adults and first-years catabolised fat during January and February 1979, average losses by first-years were greater than by adults (Figure 2). In the shorter cold spell of February 1978 some first-years but no adults catabolised fat reserves (Table 1).

The regularly recorded winter mortality of shorebirds during severe weather (Table 6) shows that nutritional reserves

are often insufficient to ensure survival. This situation can arise in two ways. Firstly, when part of a population cannot regulate its nutritional reserves (i.e. reserves are smaller than their regulated size), these birds will have insufficient reserves for survival during severe weather. This occurs in Redshanks wintering on British east coast estuaries where non-regulated loss of condition involves both adult and first-year birds. Some first-year shorebirds may also be unable to store sufficient reserves to balance their poor feeding efficiency. There is some evidence that mortality is higher in first-year than adult shorebirds during severe weather, particularly in Oystercatchers (Heppleston 1971, Baillie 1980). Secondly, during very severe weather (e.g. the 1962/63 winter) when mudflats freeze over (Ash 1964, Dobinson & Richards 1964) even regulated levels of nutritional reserves can be exhausted and heavy mortality results. This severity of weather occurs very infrequently (Dugan 1981). There are strong disadvantages in carrying large fat reserves (Paper 1), and in any case the amount of fat needed for survival through a prolonged period of starvation during very cold weather may exceed the maximum of 50% total body weight that can be carried (Pennycuick 1975). Shorebirds do not store large enough fat and muscle protein reserves for survival through the most severe weather that they can encounter on their wintering grounds. The correlations between mean monthly air temperature and total body weight during midwinter in Dunlins (Pienkowski, Lloyd & Minton 1979) and Redshanks (Figure 10) indicate that, since differences in total body weight are due mainly to differences in fat loads, on each wintering area the size of the regulated fat reserve is

related to the average weather conditions encountered in that area.

The extensive use of both fat and protein reserves during severe weather emphasises that changes in foraging behaviour (e.g. Smith 1975, Evans 1976, Pienkowski 1980a, b) are often unable to compensate for decreased food intake and increased energy requirements. Storage of nutritional reserves as insurance against these periods of high energetic and metabolic demand allows shorebirds to overwinter on estuaries such as those in eastern Britain where the severity of winter weather would otherwise cause high mortality through starvation. Winter mortality of both plovers and sandpipers in north-east England is low (Evans 1980b, Brearey 1981). Plovers, which face greatest reductions in food intake during severe weather and which store the largest nutritional reserves during winter, generally overwinter on more southerly wintering grounds than do sandpipers (Pienkowski 1980a). Conversely, rocky shore species such as Purple Sandpipers, which probably face little reduction in food intake during winter and which store small nutritional reserves (Paper 1), can overwinter as far north as Iceland and Greenland (Morrison 1976, Wilson 1981).

Are Redshanks in eastern Britain unable to maintain regulated levels of nutritional condition even during mild winters?

Redshanks might carry small fat and protein reserves in late winter if,

a) they can always feed at an adequate rate even in severe weather, as may occur in Purple Sandpipers (Atkinson et al. 1981), and so need little 'insurance' of fat and protein reserves for poor feeding conditions, or

b) their nutritional condition, in successive samples, becomes steadily worse.

Redshanks cannot always feed (e.g. Goss-Custard 1969) and they often suffer heavier mortality than other shorebirds (Goss-Custard et al. 1977, Baillie 1980). Therefore they should need to carry large fat and protein reserves, and the low reserves must be attributable to explanation (b). A steady decline in nutritional condition could arise if birds stayed in north-east England and lost fat and protein reserves, or if birds arriving from further south diluted the local wintering population thereby reducing average levels of condition indices. There is no evidence of influxes of migrants until mid or late February at Teesmouth or Lindisfarne (Figure 9), or the Firth of Forth (Symonds 1980). The Redshank population on some other estuaries such as the Clyde is resident all winter (Furness & Galbraith 1980).

The average total body weight and fat reserves of Redshanks in eastern Britain fall before any influxes occur (Figures 3 & 5). Therefore the changes in condition are a genuine loss of fat and protein reserves by resident birds. On the Forth, severe loss of condition in some resident birds had occurred by mid January (Figure 4).

If Redshanks are regulating their fat reserves in winter, total body weights in midwinter should be inversely correlated with air temperature (provided that there is a large resident component of the population), as found for Dunlins in Britain (Pienkowski, Lloyd & Minton 1979). The total body weights of Redshanks on the south and west coast of Britain in midwinter were inversely correlated with air temperature

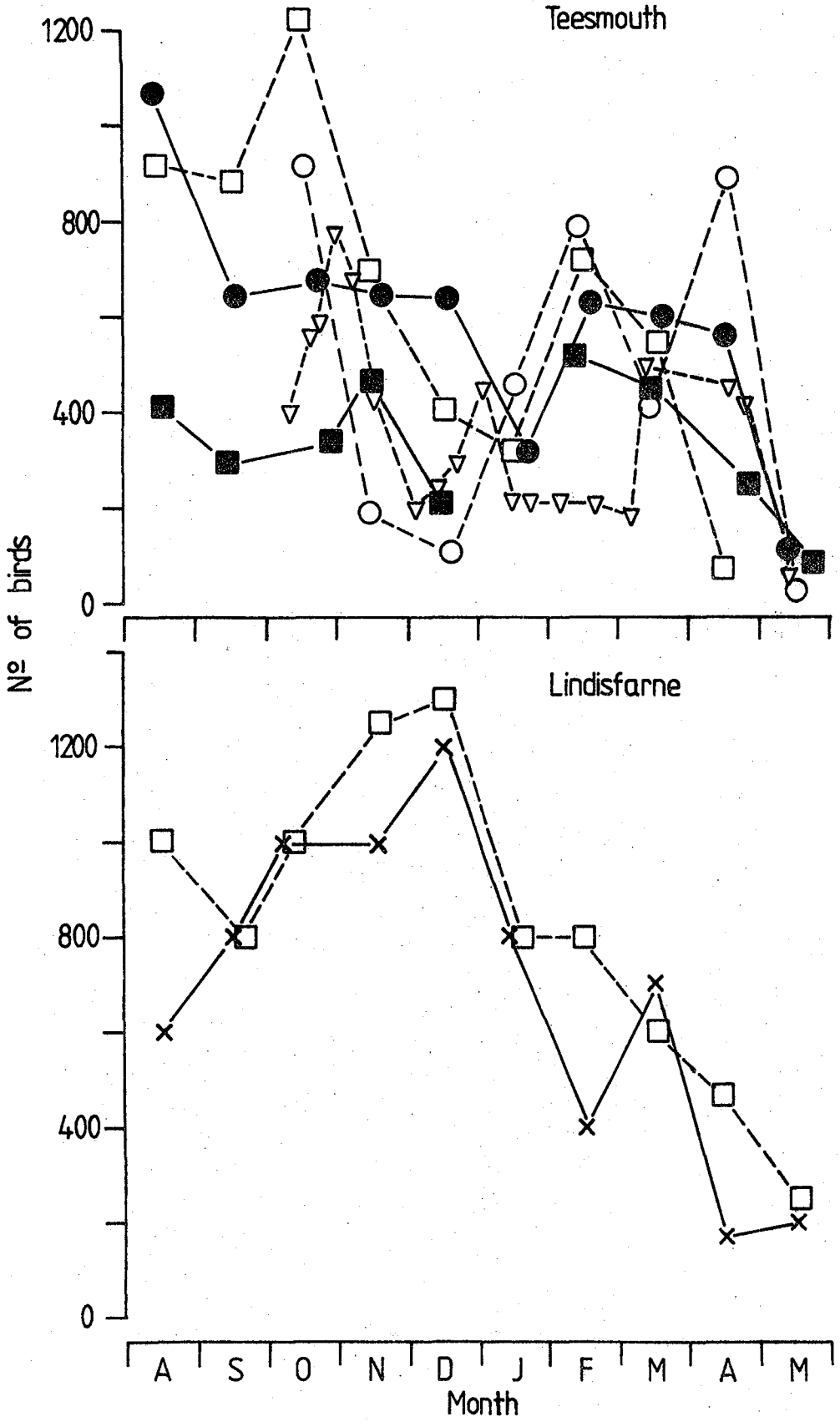

Figure 9: Population size of Redshanks at Teesmouth and Lindisfarne during various non-breeding seasons. Symbols are: x 1972/72, □ 1972/73, ■ 1975/76, o 1976/77, ● 1977/78, ▽ 1978/79. Counts for 1978/79 from Davidson (1980); all others from L.R. Goodyer and Birds of Estuaries counts made by Teesmouth Bird Club.

(Figure 10). However, weights on five east coast estuaries from the Wash to the Moray Firth were lower than predicted from the west and south coast sites (Figure 10a), suggesting that Redshanks were unable to store their required fat reserves by midwinter on the east coast of Britain. Similarly, on estuaries where the late winter decline in condition is not regulated, weights should be lower than predicted from the weights on estuaries where Redshanks are able to regulate condition. Again weights on the east coast in February were lower than predicted (Figure 10b).

If air temperature is a contributory factor in preventing Redshanks from regulating their nutritional reserves on east coast estuaries, then the weight (≡ fat) deficit below the weight predicted from west coast sites should be greatest on estuaries with the lowest temperatures. This deficit in total body weight in midwinter is inversely correlated with air temperature (Figure 11).

Non-regulated loss of reserves during even mild winters means that Redshanks should not have sufficient nutritional reserves for survival during even short periods of severe weather. Higher mortality would be predicted to occur on the east than the west coast of Britain as has been found (Pilcher 1964, Goss-Custard et al. 1977, Baillie 1980, Furness & Galbraith 1980, Furness & Baillie in press). During extended periods of severe weather, e.g. January/February 1963, high mortality of Redshanks was not confined to the east coast as it usually is (Ash 1964, Dobinson & Richards 1964).

Several proximate factors could contribute to Redshanks being more susceptible to loss of condition than other shorebirds.

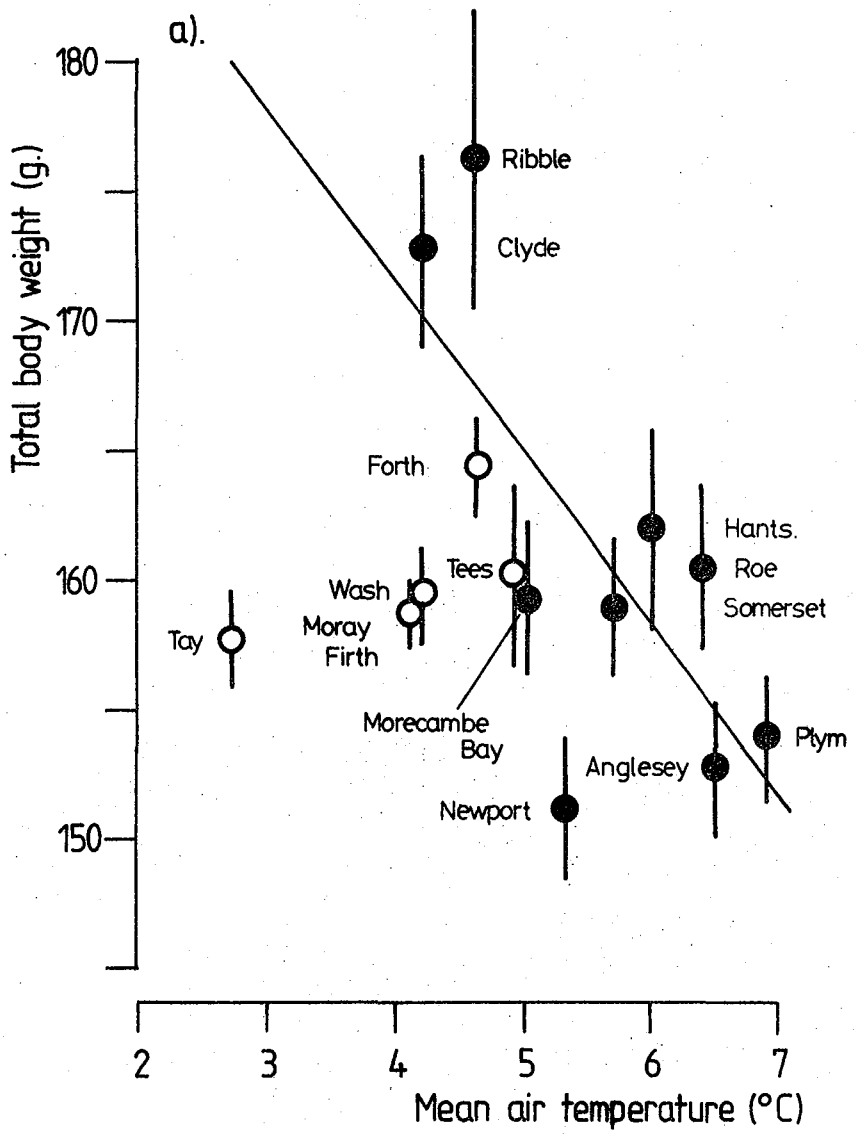

Figure 10: Total body weights of Redshanks in relation to air temperature on east coast (o) and south and west coast (•) British estuaries in a) midwinter, and b) February. Points show mean monthly weights (standardised for variations in body size) ± 1 standard error. Regressions, calculated from means from south and west coast estuaries only, are: midwinter total body weight = 197.7 - 6.55 temperature, $r_7 = -.70$, $P < .05$; February total body weight = 167.3 - 3.62 temperature, $r_5 = -.52$, $P > .10$. Air temperatures are from Meteorological Office (1976).

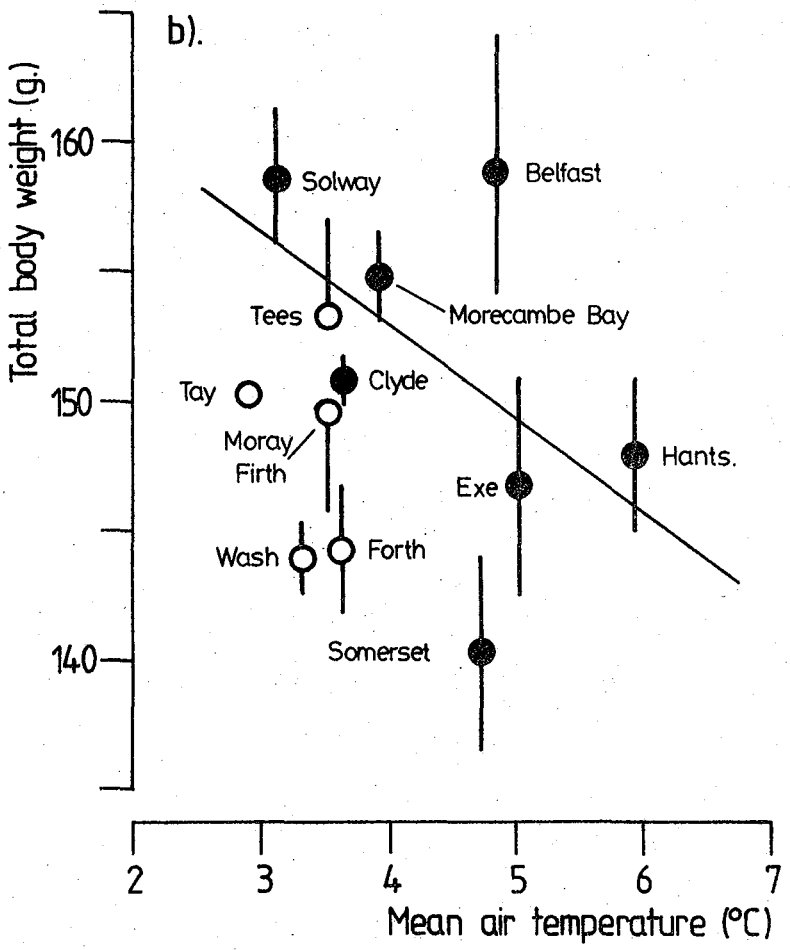
b).
Total body weight (g.)
160
150
140
Solway
Belfast
Tees
Morecambe Bay
Tay
Clyde
Moray
Firth
Hants.
Exe
Wash
Forth
Somerset
2
3
4
5
6
7
Mean air temperature (°C)

Figure 10b.

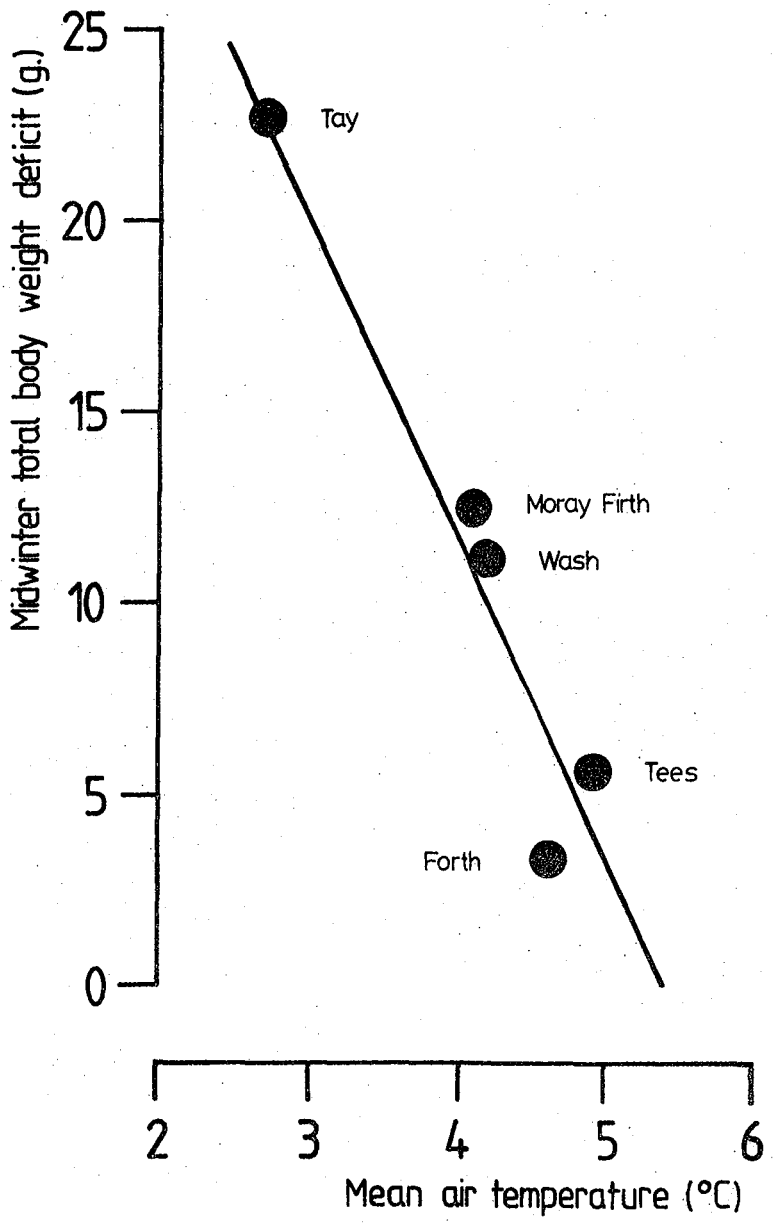

Figure 11: Midwinter deficit of the total body weight of Redshanks on British east coast estuaries in relation to air temperature. Each deficit is the difference between mean observed and predicted (from west coast estuaries) weights, from Figure 10. Regression is: weight deficit = 45.95 - 8.53 temperature, r_3 -.96, $P < .01$.

1) During mild weather in mid and late winter, Redshanks feed on mudflats for a greater proportion of the available feeding time than most other species (Goss-Custard 1969, Pienkowski 1973, Goss-Custard et al. 1977, Evans 1980a). Many Redshanks are unable to satisfy their food requirements by feeding only on mudflats and are forced to continue feeding on pastures during high water. Field-feeding occurs on the south coast of Britain (D.J. Stevenson, pers. comm.) as well as on the east coast (Goss-Custard 1969, Pienkowski 1973, Millard 1976, Davidson 1980). Field feeding over high water is more prevalent in Redshanks than most shorebirds. Therefore Redshanks cannot extend their feeding time when energy requirements are high or prey availability is low.

2) Redshanks cannot feed on open mudflats during gales because of buffeting by the wind. Redshanks wintering at Teesmouth during 1978/79 moved from the main mudflats to sheltered adjacent feeding sites during gales. At windspeeds greater than 25 knots, an average of 89% of the Tees population fed on sheltered sites during low water, compared with only 30.5% when winds averaged 20 - 25 knots (data from Davidson 1980). Numbers of Redshank that stayed on the open mudflats, rather than moving to sheltered sites, were significantly lower on days when the average windspeed exceeded 25 knots than on less windy days (less than 25 knots $\bar{x}$ = 272 birds, greater than 25 knots $\bar{x}$ = 46 birds, $t_{13} = 3.62$ $P < .01$). In contrast, few Dunlin chose to move from open mudflats to peripheral feeding areas under any weather conditions during low water, even during gales (only 7.5% of the Dunlin population moved even when winds exceeded 25 knots). In the compact flocks formed in sheltered areas during gales, Redshanks fed by touch rather than by their

preferred visual feeding and took less-preferred food items (Goss-Custard 1976), so during gales Redshanks may suffer reduced food intake as well as facing an increased cost of thermoregulation.

3) As for other shorebirds that prefer to feed visually, the availability of prey to Redshanks is reduced during cold weather because invertebrates become less active and move deeper into the substrate (Evans 1979, Pienkowski 1980a, b). In the same way as during gales, Redshanks may then have to feed by touch and suffer reductions in food intake. Similarly Redshanks feeding at night probably forage by touch and take less-preferred prey (Goss-Custard 1969).

Gales become frequent on the east coast of Britain from November to March (Dugan et al. 1981). The increased windchill caused by high winds and decreasing temperatures at this time of year, and the change to a less preferred feeding method may be sufficient to prevent Redshanks storing fat reserves after November. However this does not fully explain why other long-legged and/or visually-feeding shorebirds such as Curlews, Bar-tailed Godwits and Grey Plovers, species also buffeted by gales (Smith 1975, Davidson 1980, Townshend 1981, Dugan et al. 1981), are able to maintain regulated levels of condition on the same east coast estuaries.

It is possible that the inability of Redshanks to regulate winter nutritional condition on some estuaries results from Redshanks having a higher metabolic rate per unit weight than other shorebirds wintering in Britain. This would explain why Redshanks cannot maintain condition whilst other shorebirds

can readily achieve a positive energy balance that permits fat storage until midwinter in mild weather. Measurements of basal metabolic rate have not been published for Redshanks and other shorebirds, so metabolic rate as the ultimate factor preventing regulation of condition in eastern Britain cannot be confirmed.

Redshank are the only Tringine sandpiper which overwinters in large numbers in eastern Britain. Other congeners such as the Greenshank, T. nebularia and Spotted Redshank, T. erythropus, and the smaller Wood Sandpiper, T. glareola and Green Sandpiper, T. ocrophus overwinter chiefly in Ireland, Southern Europe and Africa (Moreau 1967, Pearson et al. 1972, Prater 1976) where weather conditions are milder. Many Redshanks also overwinter in these areas where a high metabolic rate would be unlikely to affect winter survival.

There could be several reasons for the difference in the ability of Redshanks to regulate condition on the east and west coasts of Britain:

1) Higher percentages of first-year Redshanks occur on east coast estuaries than on the west coast (Furness & Baillie in press). Since first-year shorebirds have lower average feeding efficiencies than adults, a higher proportion of the east coast populations should be unable to achieve an energy balance when weather conditions deteriorate. However, I have shown that many adult Redshanks are also unable to regulate nutritional condition on some east coast estuaries (Figure 4), so this age-difference in distribution is probably unimportant.

2) Differences in body size and racial origin of the wintering populations can be excluded. On both east and west coasts, average body size is similar and both British and Icelandic Redshanks winter on each estuary (Furness & Baillie in press). On some south coast estuaries Redshanks are much smaller and are probably British breeding birds. However, these populations, like those on the west coast, are able to regulate condition (Figure 10).

3) Weather conditions on east coast estuaries are more severe than on west coast estuaries, during both normal winters and severe weather. Dugan (1981) has reviewed temperatures and wind speeds and has shown that mid and late winter air and sea temperatures were lower on east coast estuaries in both mild winters and the few recent severe winters. Although strong winds are more frequent in the west than in the east, windchill (upon which the energetic requirements for thermoregulation depend) is highest on the north-east coast of England in mid-winter even during mild weather. During severe January weather in 1963 and 1979, windchills were also higher on the east than west coasts of Britain. The higher energy requirements for thermoregulation on the east coast in midwinter, when Redshanks cannot feed on their preferred feeding grounds or by their preferred foraging method is probably the main cause of the differences in the ability of Redshanks to regulate nutritional condition on the east and west coasts of Britain.

SUMMARY

The use of nutritional reserves by shorebirds was examined during two periods of severe winter weather in north-east England. Nutritional condition at death from starvation during severe weather was reviewed, using mainly published sources. The use of both fat and protein reserves during severe weather varied interspecifically: catabolism of reserves was more frequent and more extensive in plovers (Charadriidae) than sandpipers (Scolopacidae). Some sandpipers (e.g. Dunlins and Bar-tailed Godwits) did not catabolise reserves during some periods of severe weather. In contrast to other shorebirds, and Redshanks in western Britain, some Redshanks wintering in eastern Britain cannot regulate their nutritional condition even during mild winters. These birds had very low fat reserves by late winter and by then had also used muscle protein. The reasons for non-regulated loss of condition in Redshanks are not fully understood. Redshanks and first-year Oystercatchers suffer higher winter mortality than other estuarine shorebirds. During winter inland feeders, particularly Lapwings, also have a high risk of mortality during severe weather as do many shorebirds that return to their breeding grounds early in spring. By death, protein reserves have been extensively catabolised, as have all fat reserves. The extent of protein catabolism before death depends on the severity of the weather conditions. Shorebirds can recover condition rapidly from lean weights close to those at which they die.

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Paper 3. Seasonal and geographical variation in the lean weights of shorebirds (Charadrii)

INTRODUCTION

Most major changes in the total body weight of shorebirds (Johnston & McFarlane 1967, Mascher & Marcstrom 1976, Dugan et al. 1981, Paper 1), as in other birds (e.g. King & Farner 1959, Hanson 1962, Blem 1966, 1976, King 1972), are due to changes in the weight of stored lipids used chiefly as an energy reserve. These changes are normally of sufficient size to mask any changes in lean body components such as water and muscle outside the moult period.

Protein reserves, particularly in the pectoral and sometimes the leg muscles, are used during breeding for egg production, during moult, and as a source of amino-acids for protein synthesis when feeding is impossible. Such reserves have been found in Quelea Quelea quelea (Kendall, Ward & Bacchus 1973, Jones & Ward 1976) and geese (Hanson 1962, Ankney 1977), and are known to vary seasonally. In shorebirds, protein reserves are used when feeding is impossible because of high winds and low temperatures (Evans & Smith 1975, Dugan et al. 1981, Papers 1 & 2).

Most shorebirds regulate both fat and protein reserves in winter (Dugan et al. 1981, Paper 1). The size of regulated fat reserves on different wintering grounds is correlated with the severity of the weather conditions in each area (Pienkowski, Lloyd & Minton 1979, Papers 1 & 2).

In Papers 1 and 2 I have documented the seasonal changes in fat and protein reserves in one northern temperate wintering area, north east England. Seasonal changes in the fat reserves

of shorebirds have been reported also from various tropical and southern hemisphere wintering grounds (Johnston & McFarlane 1967, McNeil 1970, Baker 1975).

Outside the northern temperate region few studies have examined the protein reserves of shorebirds, usually measured as indices of pectoral muscle size (Evans & Smith 1975, Paper 1), other than Elliott et al. (1976) who report pectoral muscle weights of Curlew Sandpipers, Calidris ferruginea, in South Africa. However total lean weight follows the same seasonal pattern as pectoral muscle size in north-east England (Evans & Smith 1975, Paper 1) and seasonal changes in lean weight elsewhere are reported by Johnston & McFarlane (1967), McNeil (1970) and Page & Middleton (1972).

Since both fat and protein reserves are regulated and periods of high demand for both reserves generally coincide (Paper 1), seasonal and geographical differences in the size of protein reserves should be similar to those of fat reserves. This paper examines the variations in the lean weight of shorebirds at different latitudes and in different seasons. Latitudinal differences in lean weight at the same time of year clearly involve different birds, whereas seasonal differences at any one site could result either from changes in the lean weight of resident individual birds at that site, or from turnover of populations (or both). In published data, it is not possible to differentiate between these last two effects, other than in north-east England where most seasonal changes in condition are those of individuals (Paper 1).

The study is limited to those species of Charadrii that are migratory and breed in the Holarctic region, and to those species that are associated chiefly with intertidal habitats during the non-breeding season. Waders that spend the non-

breeding season away from coastal areas are not discussed because they are subject to different environmental conditions which could affect lean weight levels.

METHODS

Samples of shorebirds have been collected during the last ten years at Teesmouth and Lindisfarne, north-east England during studies of diet (Evans et al. 1979), nutritional condition (Evans & Smith 1975, Dugan et al. 1981, Papers 1 & 2) and heavy metal pollution (Evans & Ward in prep.). Most samples were collected during the northern winter (November - March), with fewer samples in autumn (August - October) and spring (April - May). A sample of Redshank, Tringa totanus, from the Ythan estuary, north-east Scotland, was also examined. Carcasses were weighed and then deep-frozen until required. Methods of condition analysis are described by Evans & Smith (1975) and in Paper 1. Total lean weight was calculated as the weight of lipids subtracted from the total body weight.

Other lean weights have been calculated from published information. The methods of carcass analysis used by McNeil (1970) differ markedly from those used in this study. So that lean weights are comparable, those from McNeil (1970) have been corrected by the addition of 11.5%, calculated from three species for which McNeil (1970) gives weights of fat and total body weights comparable to those from other studies.

Wing-length is the most widely available measurement that is correlated with body size in shorebirds (McNeil & Cadieux 1972, Page & Middleton 1972, Baker 1975, Mascher & Marcstrom 1976). Few wing-lengths are available in association with lean weight

samples in the literature. Where wing-lengths are not given in the relevant paper, mean wing-lengths for the species or subspecies have been taken from Prater, Marchant & Vuorinen (1977), where possible adjusted for the sex ratio of each sample since most shorebirds are sexually dimorphic in size. The wing-lengths given in Prater, Marchant & Vuorinen (1977) were measured from museum skins, and because some shrinkage occurs when skins are dried (for reasons see Knox 1980), these wing-lengths have been corrected using an average value of 2.5% shrinkage (Greenwood 1979, Green 1980). The wing-length used throughout this study is the flattened, straightened chord (Evans 1964), the measure used by most British workers. Some authors have measured flattened chord: these wing-lengths have been corrected using a difference of 3.3% calculated from Pienkowski, Lloyd & Minton (1979). Wing-length is not an ideal measure of body size since wing-length decreases with increasing feather age (Pienkowski & Minton 1973) and is subject to measurement errors. No other body size measurement is sufficiently widely available for use. However the size and shape of all shorebirds are very similar and most variation occurs in the hind limbs (Bucher 1978).

For analysis, because weight is expected to vary in proportion to a volumetric measure but wing-length a linear parameter, weights have been transformed to their cube roots. Weights in some previous studies (e.g. McNeil & Cadieux 1972, Mascher & Marcstrom 1976) were not transformed. These untransformed relationships are curvilinear, although not markedly so over the size range of a single species. Relationships between wing-length, and lean weight have been analysed using bivariate regressions.

RESULTS

Lean weights in winter

The relationship between the mean wing-length and mean lean weight of all shorebird species measured in north-east Britain during November - March is shown in Figure 1. Correlations for both adults (r_7 = .9991 b = .0294 P<.0001) and first-years (r_2 = .9995 b = .0294 P = .0005) are highly significant. The plovers, Pluvialis squatarola, P. apricaria and Charadrius hiaticula conform to the same regression equation as sandpipers (Scolopacidae). The slopes of the regressions for adults and first-years are identical but the intercepts differ. However, this difference is not significant. Within single species, first-year Redshanks and Bar-tailed Godwits, Limosa lapponica, had significantly shorter winglengths and lower lean weights than adults (Student's t, P<.05).

Lean weights from equatorial and southern hemisphere wintering areas during November - February are shown in Figure 2. Weights from March have been excluded from the "winter" data from these areas, because spring migration begins earlier than in northern temperate areas (McNeil 1970, Summers & Waltner 1979). The correlations for shorebirds wintering in southern Africa and various other areas (r_5 = .9994 b = .0292 P<.0001) and in Venezuela (r_8 = .9893 b = .0271 P<.0001) are both highly significant. As in north-east Britain during winter, in southern wintering areas plovers conform to the same regressions as sandpipers. Lean weights in all equatorial and southern temperate wintering areas are lower than the winter lean weights in north-east Britain, although the only significant difference is between southern Africa and first-years in north-

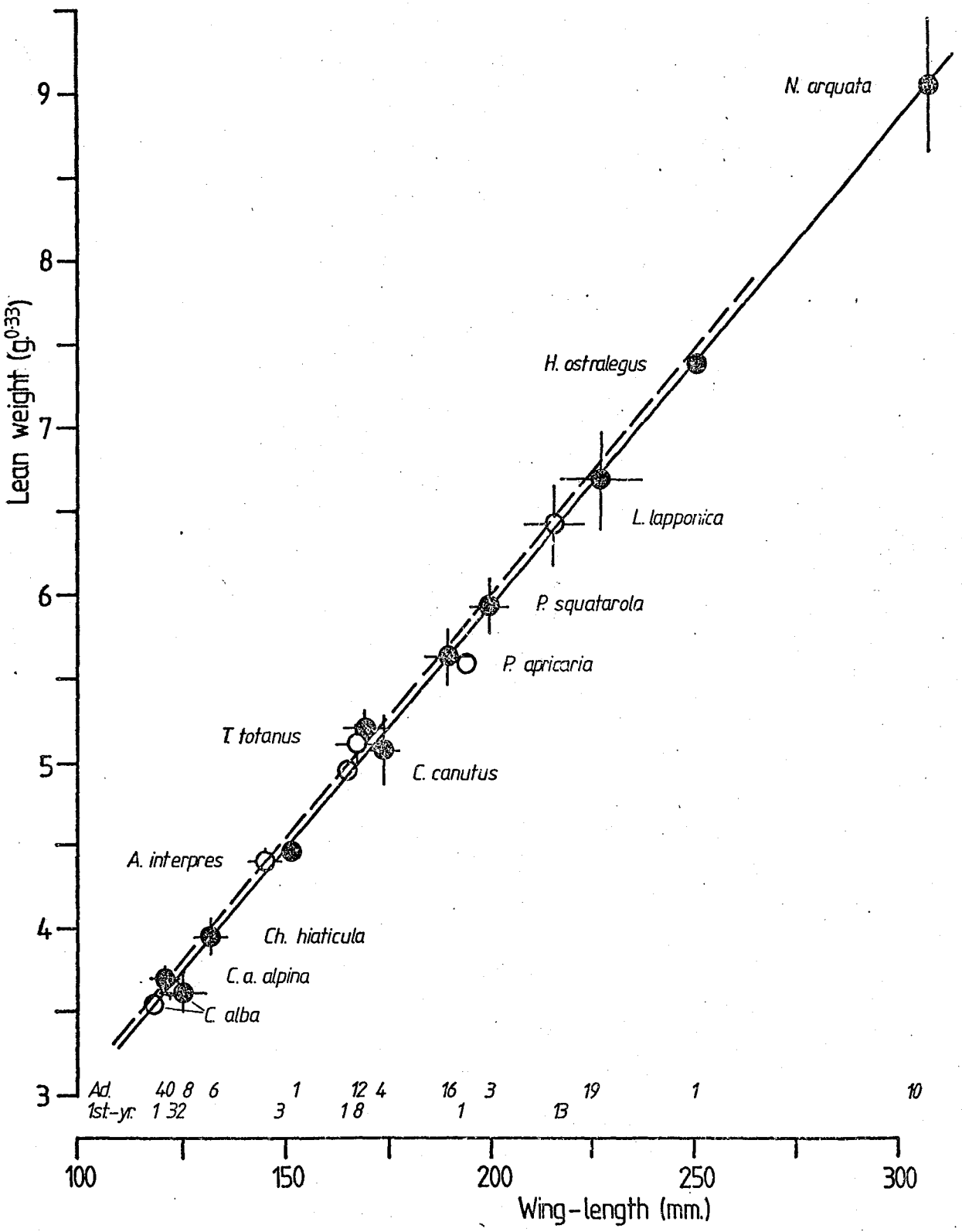

Figure 1. The relationship between lean weight and wing-length for adult (●) and first-year (○) shorebirds wintering (November - March) in north-east Britain. Each point is the mean ± 1 standard error, and numbers indicate sample sizes. Least-squares regression lines calculated from mean values (excluding single specimens) are shown for adults (———) and first-years (-----). Abbreviations of genera in this figure and Figures 2 - 6 are: A. = Arenaria, Ac. = Actitis, C. = Calidris, Ca. = Catatrophorus, Ch. = Charadrius, H. = Haematopus, He. = Heteroscelus, L. = Limosa, Li. = Limnodromus, M. = Micropalama, N. = Numenius, P. = Pluvialis, and T. = Tringa.

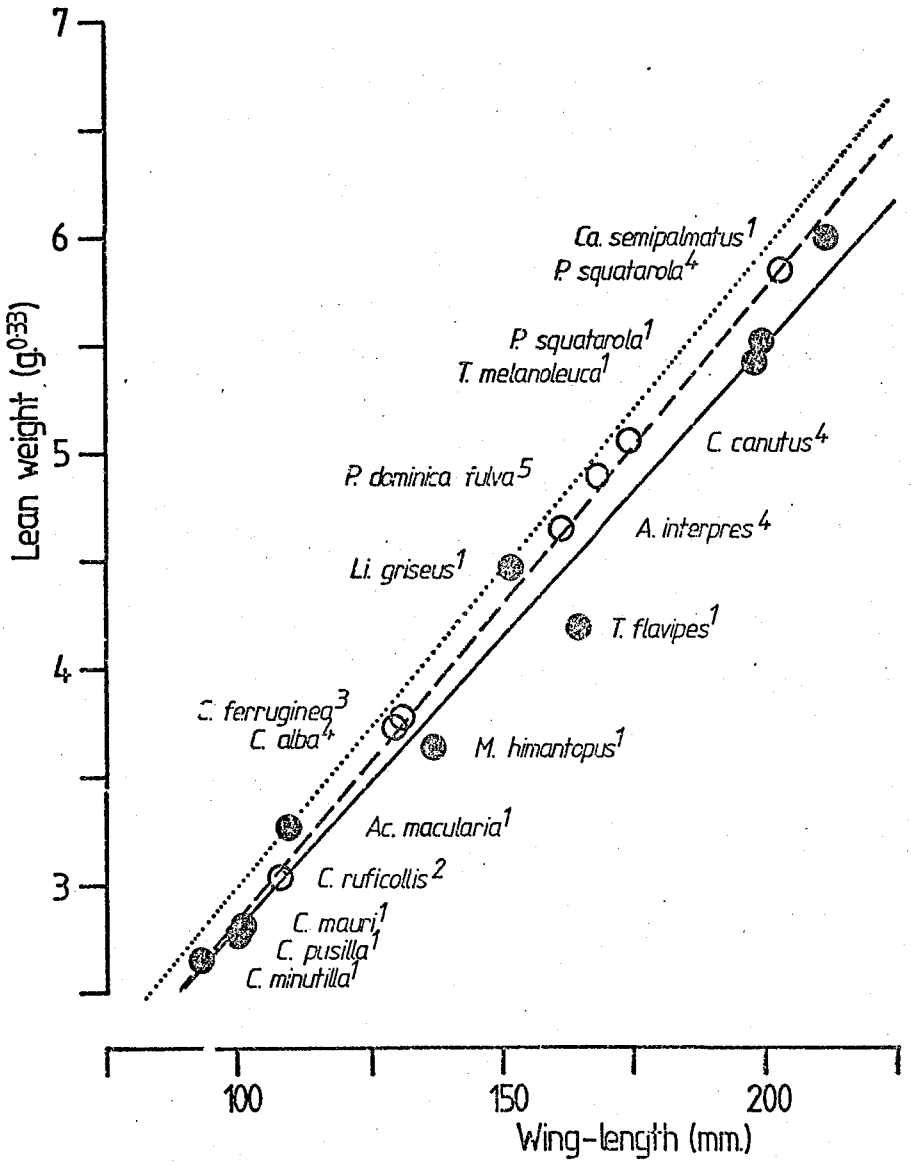

Figure 2. The relationship between lean weight and wing-length for shorebirds wintering (November - February) in equatorial and southern hemisphere areas: Venezuela (•), and southern Africa, Tasmania and Wake Island, Pacific Ocean (o). Points show the mean value for each species, and superscript numbers indicate sources of lean weights: 1 McNeil (1970), 2 Thomas & Dartnall (1970) (adjusted by the addition of 9 g. - see Paton & Wykes (1978)), 3 Elliot et al. (1976), 4 Summers & Waltner (1979), and 5 Johnston & McFarlane (1967). Least-squares regression lines are shown for Venezuela (———), Africa, Tasmania and Wake Is. (-----), and adults wintering in north-east Britain (.....). See Figure 1 for abbreviations of genera.

east Britain (t_{11} = 3.44 $P < .01$). In southern Africa the lean weights of adults are 7% lower in Grey Plovers, 6% lower in Knot, Calidris canutus, and 3.5% higher in Sanderling, Calidris alba, than in north-east Britain. In an adult shorebird with a wing-length of 150 mm., lean weight in Venezuela (10°N) is 20% less, and in southern Africa (33°S) is 10% less, than in north-east Britain (55°N). The slopes of the regression lines are not significantly different, although this could be partly due to increased standard errors on the regressions for southern wintering areas, caused by the additional errors in measuring and estimating wing-lengths for these samples (see Methods).

Lean weights during migration

Much of the published information on the lean weights of shorebirds refers to birds caught during southwards autumn migration through the northern temperate regions. Lean weights of different species in relation to body size (wing-length) during autumn (August - October) in the northern temperate region are shown in Figure 3. The correlations for both adults (r_9 = .9919 b = .0284 $P < .0001$) and first-years (r_5 = .9922 b = .0296 $P < .0001$) are again highly significant. The lean weights of neither adults nor first-years differ significantly from those of the respective age-class during winter (November - March) in north-east Britain, but the differences are large: for a shorebird of 150 mm. wing-length, lean weights in autumn are apparently lower by 12% in adults and 13.5% in first-years. In first-years the slope of the regression is slightly, but not significantly steeper than that of adults (t_{18} = 0.58 $P > .10$), and the slopes of the regressions for each age-class do not differ significantly between autumn and winter (Student's t, both $P > .10$).

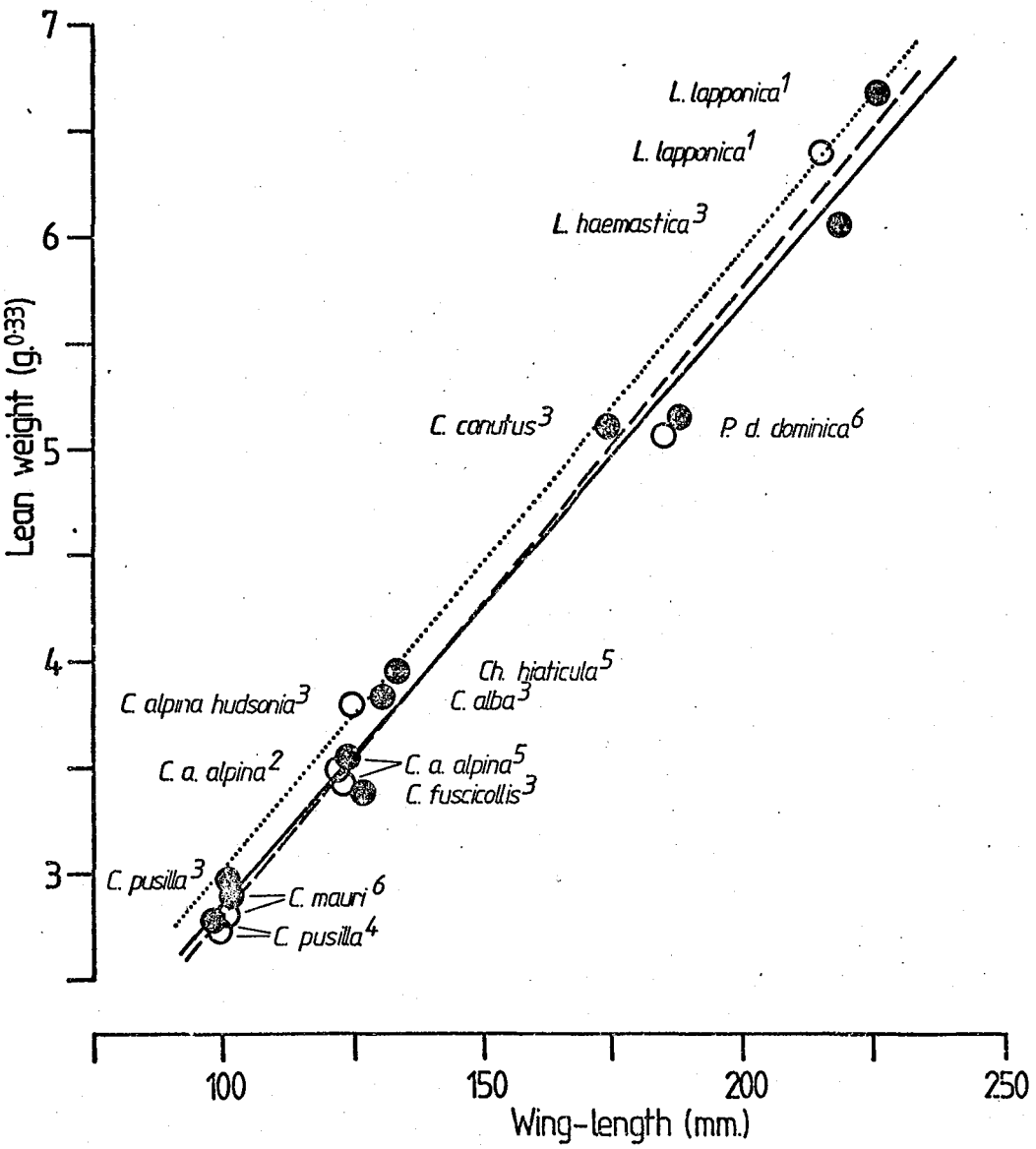

Figure 3. The relationship between lean weight and wing-length for adult (●) and first-year (o) shorebirds in the northern temperate region during autumn (August - October). Points show the mean value for each species, and superscript numbers indicate sources of lean weights: 1 Evans & Smith (1975), 2 Mascher & Marcstrom (1976), 3 McNeil & Cadieux (1972), 4 Page & Middleton (1972), 5 Paper 1, 6 Johnston (1964). Least-squares regression lines are shown for adults (———), first-years (-----), and adults wintering in north-east Britain (.....). See Figure 1 for abbreviations of genera.

The only published lean weights from south of the northern temperate region during autumn migration are from Venezuela (McNeil 1970). The correlation between wing-length and lean weight is shown in Figure 4, and is highly significant (r_{10} = .9805 b = .0287 P< .0001). For a shorebird with a wing-length of 150 mm., the autumn lean weight in Venezuela is 11% lower than the lean weight in the northern temperate region during autumn, and 1% lower than the winter lean weight in Venezuela. Neither of these differences is significant, nor does the slope significantly differ from that of other seasons and areas.

A series of total body weights is available from Mauritania North-west Africa, during October (Dick 1975, Dick & Pienkowski 1979),a period when most shorebirds would have carried little fat because they had only recently arrived in the area on migration from further north. Figure 5 shows the correlations between wing-length and total body weight. As with lean weights elsewhere, the correlations are highly significant (adults r_{10} = .9974 b = .0287 P<.0001; first-years r_8 = .9819 b = .0290 P<.0001). Total body weights in Mauritania are slightly higher than the autumn lean weights in the northern temperate region, but since at least 1.5% of the total body weight will have consisted of lipids (Paper 2) it is probable that the lean weights in Mauritania in October are lower than those further north in autumn. This would be consistent with Pennycuick's (1978) suggestion that some protein reserve, probably muscle, is used during migration. First-years of 150 mm. wing-length have 3.5% lower fresh weights than adults, although this difference could be due in part to age-related differences in lipid levels (Paper 1). The slope of the regression line is slightly, but not significantly steeper than that of adults.

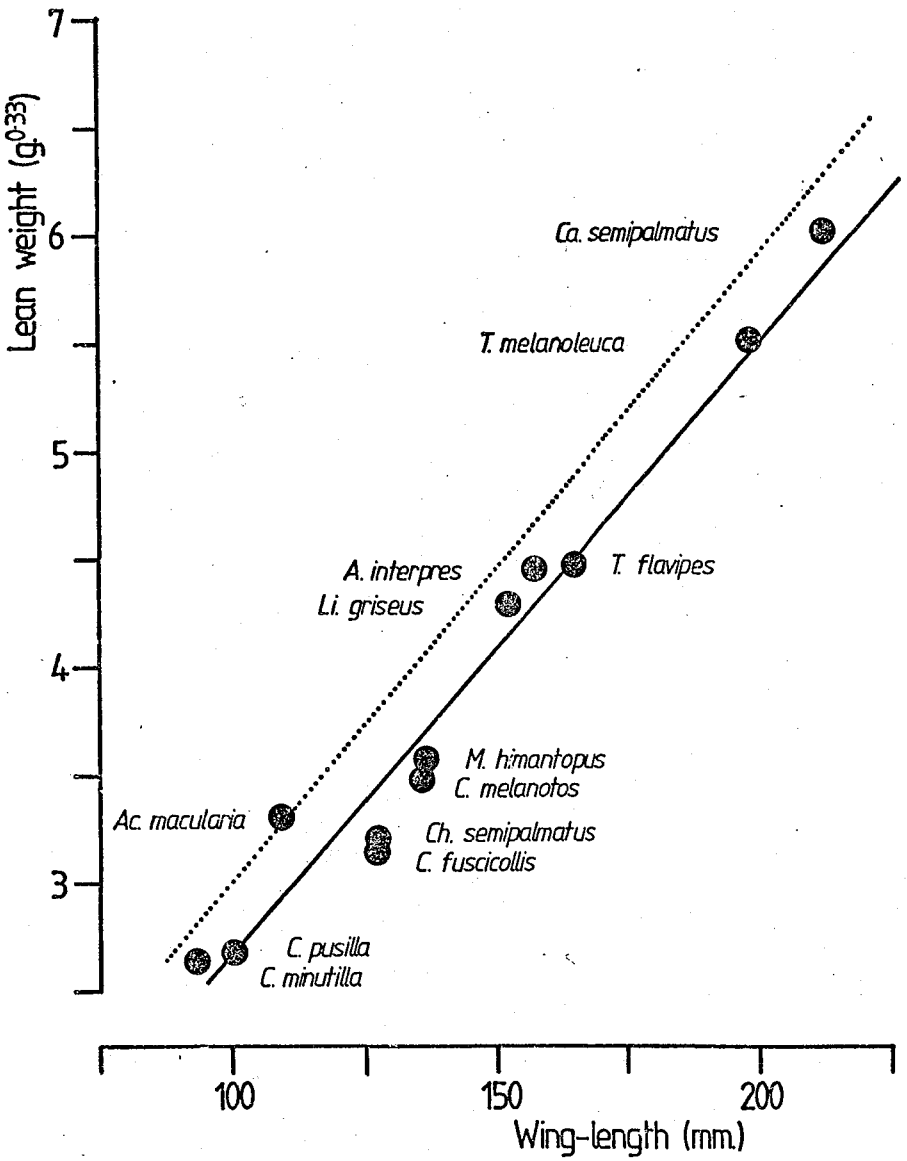

Figure 4. The relationship between lean weight and wing-length for shorebirds in Venezuela in autumn (August - October). Lean weights are calculated from McNeil (1970). Least-squares regression lines are shown for Venezuela (———), and adults wintering in north-east Britain (.....). See Figure 1 for abbreviations of genera.

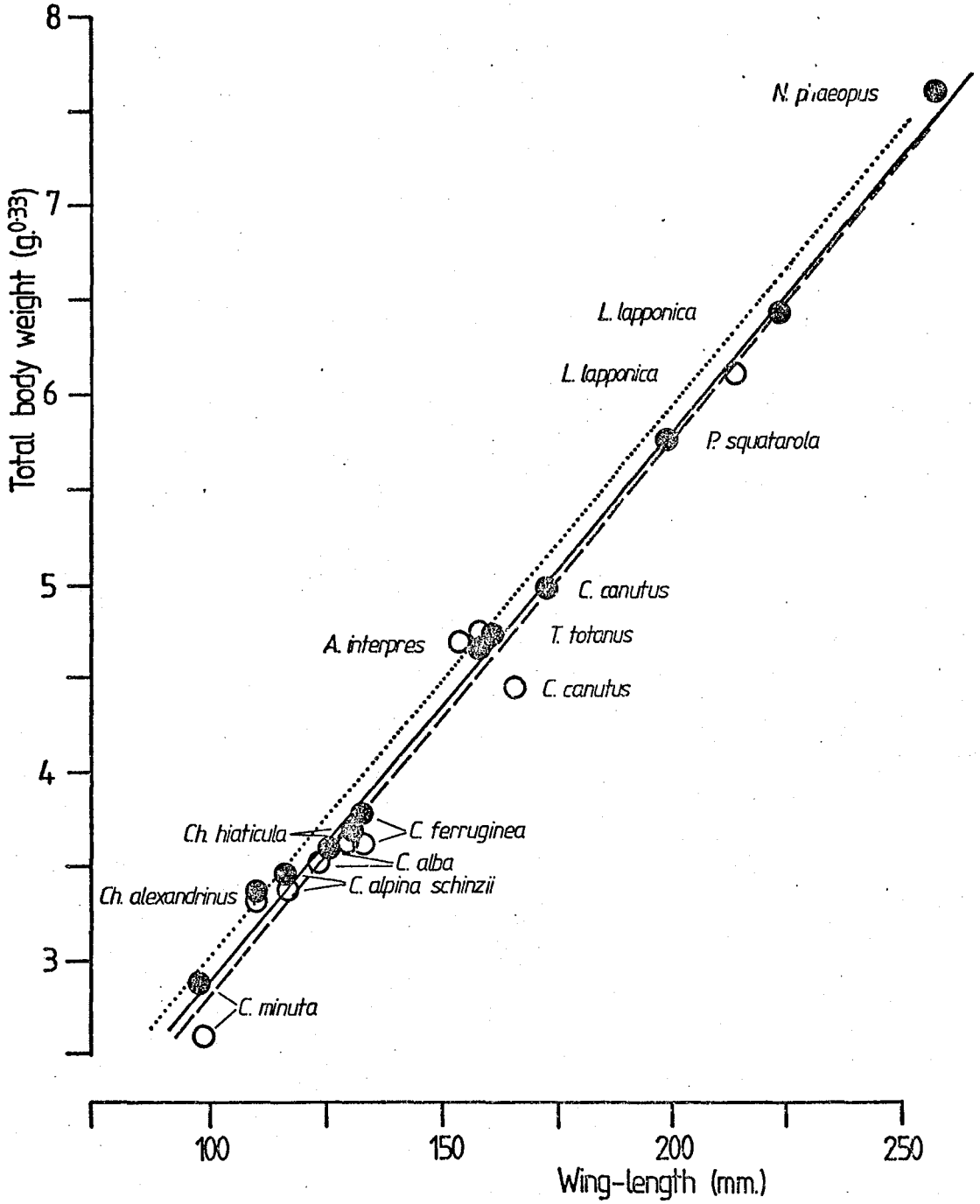

Figure 5. The relationship between total body weight and wing-length for adult (●) and first-year (o) shorebirds in Mauritania in October. Points show the mean value for each species. Values are from Dick (1975) and Dick & Pienkowski (1979). Least-squares regression lines are shown for adults (———), first-years (-----), and adults wintering in north-east Britain. See Figure 1 for abbreviations of genera.

There is limited information available for lean weights during spring migration (April - May). Evidence from species for which data are available from both winter (November - February/March) and spring in the same area indicates that lean weight increases from winter to spring by up to 13% (Table 1).

There is no evidence that the percentage increase in lean weight before spring migration in shorebirds over-wintering in equatorial and southern temperate regions is greater that in shorebirds wintering further north. Since winter lean weights are lower in the south than in the north, it appears that shorebirds wintering in these southern wintering areas must further increase their lean weights after departing from their wintering grounds. Lean weight increases rapidly within a few weeks in spring (McNeil 1970, Paper 1). This makes more detailed analysis of spring lean weights unrealistic with the existing state of information since lean weights can vary markedly depending on the length of stay of each bird at a migration stopover.

Lean weight in summer on wintering grounds

Lean weights of non-breeding shorebirds during summer (June-July) on wintering grounds are available from two equatorial areas: Enewetak Atoll (11°N) in the Pacific Ocean (Johnson & Morton 1976) and north-east Venezuela (10°N; McNeil 1970). Correlations between wing-length and lean weight (Figure 6) are significant in both areas (Venezuela $r_9 = .9909$ $b = .0278$ $P < .0001$; Enewetak Atoll $r_2 = .9920$ $b = .0289$ $P < .01$) and the lean weights are similar in both areas: a shorebird with a wing-length of 150 mm. has a 3.5% higher lean weight on Enewetak Atoll than in Venezuela. Neither this, nor

Table 1. Premigratory increases in the lean weight of shorebirds on various wintering areas in spring.

Species	Age	Sex	Area	Latitude	Winter Lean Weight (g.)	Spring Lean Weight (g.)	% Change	Source
Limosa lapponica	1st-yr.	male	Lindisfarne, N.E. England.	55°40'N	262.8	282.0	+ 7.3	1
	1st-yr.	female			313.4	311.0	- 0.8	1
Calidris a. alpina	ad.	male	Teesmouth, N.E. England.	54°35'N	47.9	53.4	+11.5	2
	ad.	female			52.0	56.8	+ 9.2	2
	1st-yr.	male			46.3	50.8	+ 9.7	2
	1st-yr.	female			51.2	57.7	+12.7	2
C. alba	ad.				48.2	54.6	+13.3	2
Pluvialis dominica fulva	ad.	male	Wake Island, Pacific Ocean.	19°17'N	116.4	124.6	+ 7.0	3
	ad.	female			112.4	127.8	+13.7	3
Pluvialis squatarola	*	*	North-east Venezuela.	10°30'N	150.0	175.0	+16.7	4
Actitis macularia					31.1	33.5	+ 7.7	4
Tringa melanoleuca					141.7	160.0	+12.9	4
T. flavipes					66.0	71.2	+ 7.9	4
Catatrophorus semipalmatus					193.5	200.0	+ 3.4	4
Calidris minutilla					16.5	18.5	+12.1	4
C. pusilla					19.0	19.6	+ 3.2	4
C. mauri					20.0	21.0	+ 5.0	4
Limnodromus griseus					80.0	90.0	+12.5	4
Micropalama himantopus					42.7	47.5	+11.2	4

Sources: 1. Evans & Smith (1975); 2. Present Study; 3. Johnston & McFarlane (1967); 4. McNeil (1970).

* Ages and sexes of samples from Venezuela unknown.

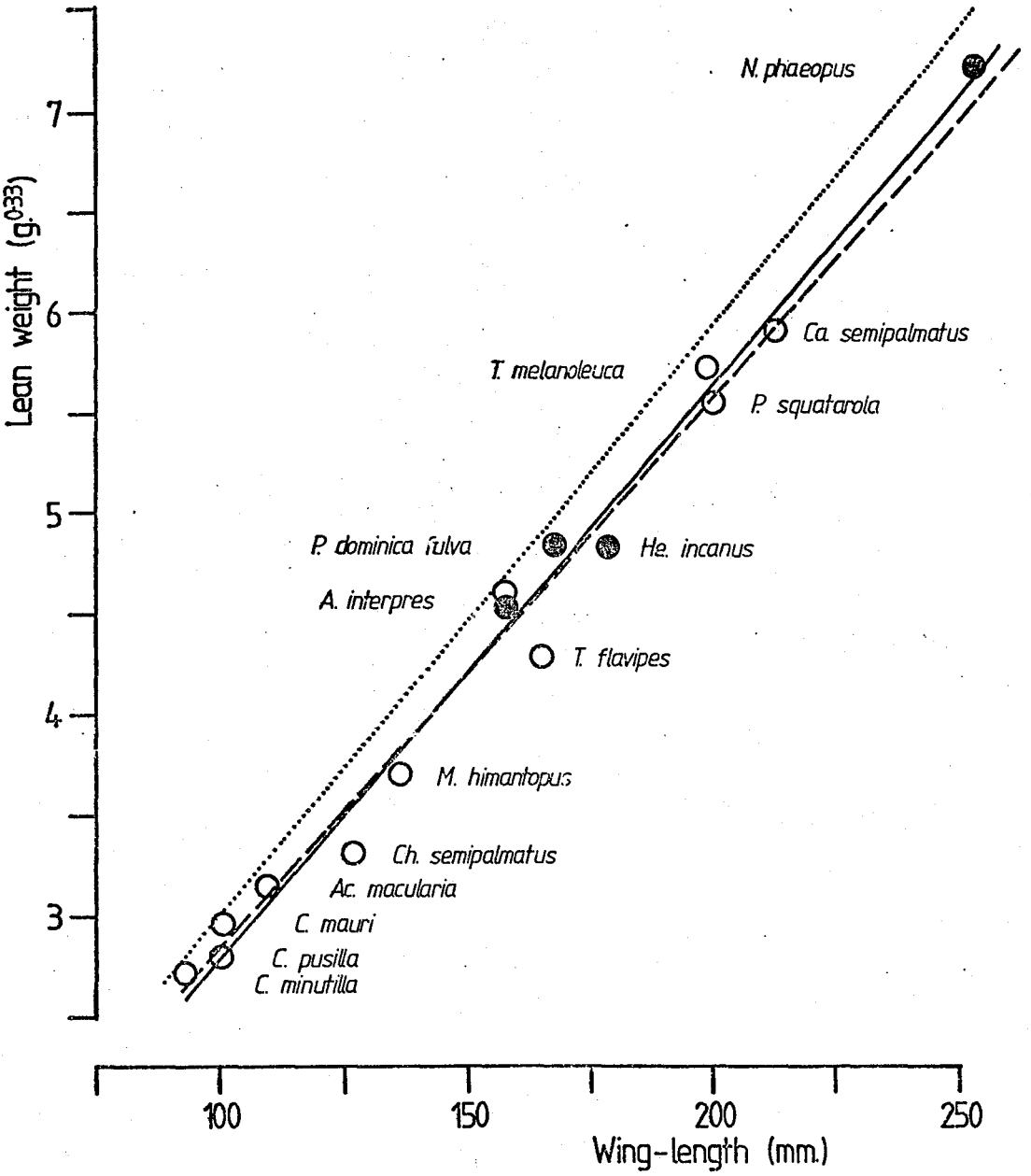

Figure 6. The relationship between lean weight and wing-length for shorebirds summering (June - July) on Enewetak Atoll, Pacific Ocean (•) with data from Johnson & Morton (1976), and in Venezuela (o) with data from McNeil (1970). Points show the mean value for each species. Least-squares regression lines are shown for Enewetak Atoll (——), Venezuela (- - - -), and adults wintering in north-east Britain. See Figure 1 for abbreviations of genera.

the slopes of the regression lines are significantly different. There is no information on the lean weights of shorebirds summering on northern temperate wintering grounds.

Lean weight on the breeding grounds

Little has been published on the lean weights of shorebirds on the breeding grounds during summer. In Least Sandpipers, Calidris minutilla, breeding near Churchill, Manitoba (Yarbrough 1970), the lean weight of adult males changed little between early June and late July, but adult females during the same period lost 13% of their lean weight. This decrease in the lean weight of females during breeding fits with the pattern found in other orders of birds (Hanson 1962, Jones & Ward 1976, Ankney 1977), namely that females, because of an additional protein requirement for egg production, use more of their protein reserve during breeding than males. Incubation is shared by both sexes in the Least Sandpiper (Pitelka, Holmes & Maclean 1974), and as the lean weight of females continues to decrease after egg-laying, some protein may also be metabolised during incubation, although in this case males might also be expected to lose lean weight during incubation. Dunlins, C. alpina pacifica in the same area (Yarbrough 1970) lost 9.5% of their lean weight during the same period.

DISCUSSION

The components of lean weight changes

Changes in lean weight could be due to any of its major components: protein, water and the skeleton. Changes in skeletal weight are unlikely to be responsible for major changes

in lean weight, although skeletal growth could account for part of the lean weight increase in juveniles during autumn and winter. Skeletal growth cannot account for lean weight changes in adults, nor is skeletal loss likely to contribute to lean weight losses in breeding females (Ankney & Scott 1980).

Much of the change in lean weight is due to a change in the total weight of body water, since water comprises between 65% and 70% of the lean weight of shorebirds. (The actual percentage depends mainly on the methods of carcass analysis employed, and in particular the oven temperatures at which carcasses were dried in different studies, e.g. Mascher & Marcstrom (1976), Pienkowski, Lloyd & Minton (1979), Paper 1.) However, under many circumstances the total water load changes in proportion to changes in lean dry body components, so that water remains a constant percentage of lean weight. Shorebirds that had starved to death during winter, losing up to 40% of their normal lean weight, had the same percentage water content as birds in normal condition (Marcstrom & Mascher 1979, Baillie 1980, Paper 2). In passerines, similar constancy in water content was reported by Evans (1969) in Redpolls, Carduelis flammea, that had starved to death in captivity, and by Ward (1969a) in the tropical bulbul, Pycnonotus goiavier, kept overnight without food. Among passerines, the proportion of water during migratory flight has been variously reported as remaining constant (Odum, Rogers & Hicks 1964, Child 1969) and being highly variable (Moreau & Dolp 1970). Moulting passerines often contain a higher proportion of body water than non-moulting birds (Newton 1968, Evans 1969), although in shorebirds Evans & Smith (1975) found

no evidence of a marked change in body water in moulting Bar-tailed Godwits. Water also generally forms a constant proportion of lean weight regardless of lipid levels in shorebirds and others (Odum, Rogers & Hicks 1964, Newton 1969, Page & Middleton 1972). The level of body water is thus generally related to the total lean weight and so cannot be the underlying cause of many lean weight changes.

Changes in lean dry weights (and therefore the protein component of lean weight if skeletal weight is constant) have been demonstrated in passerines on long migratory flights (Odum, Rogers & Hicks 1964, Rogers & Odum 1966, Johnston 1968, Child 1969) even before lipid reserves have been exhausted (Evans 1969). Shorebirds that had starved to death also had marked decreases in their lean dry weights; 27% in Redshanks in winter (unpublished data), 45% in Lapwings, Vanellus vanellus, and 35% in Oystercatchers, Haematopus ostralegus in spring (Marcstrom & Mascher 1979).

Many of the normal seasonal changes in the lean weight of shorebirds can also be attributed to changes in the lean dry weight. In Dunlin, Calidris a. alpina at Teesmouth (Table 2a), the lean dry weights of both adults and first-years increased significantly between autumn (September) and winter (November - March), and again between winter and spring (May). The lean dry weights of first-years in southern Sweden in September (Mascher and Marcstrom 1976) were very similar to those at Teesmouth in the same month. Sanderling, Calidris alba also increased their lean dry weight significantly between winter and May at Teesmouth ($t_9 = 3.10$ $P < .02$). Pacific Golden Plover, Pluvialis dominica fulva on Wake Island in the Pacific Ocean (Johnston &

Table 2. Lean dry weights (g.) and pectoral muscle indices (muscle weight as a proportion of a standard muscle volume - see Paper 1) of Dunlins Calidris a. alpina at Teesmouth, north-east England.

	Adult		First-year	
	Male	Female	Male	Female
a) Lean Dry Weight:				
September		14.67 ± 0.17(17) ***		13.55 ± 0.24(3) ***
November - March	15.43 ± 0.22(31) **	16.95 ± 0.23(33) ***	14.94 ± 0.23(16) **	16.68 ± 0.15(30) **
May	17.86 ± 0.84(5)	18.92 ± 0.40(6)	16.78 ± 0.52(5)	18.41 ± 0.52(5)
b) Pectoral Muscle Index (SMV):				
September		.255 ± .006(7)		.259 ± .004(3)
November - March	.274 ± .005(32) ***	.269 ± .005(32) ***	.266 ± .005(14) ***	.267 ± .004(28) ***
May	.321 ± .010(5)	.321 ± .012(6)	.310 ± .010(5)	.320 ± .010(5)

Notes: 1. Values are the mean ± 1 standard error, with the sample size in parentheses.
2. See Paper 1 for the methods of calculating the Pectoral Muscle Index (SMV).
3. Significant differences (Student's t tests) are: * < .05, ** < .01, *** < .001.

McFarlane 1967) showed lean dry weight increases between August and December, and December and April. The percentage increases in lean dry weight between winter and spring are similar in Pacific Golden Plovers (12.5%) on Wake Island, and adult Sanderlings (13.5%) and adult Dunlins (females 11.5%, males 15.5%) at Teesmouth.

Part of the spring increase in Dunlin lean dry weight is an increase in pectoral muscle size (Table 2b), consistent with increased protein storage for migration and breeding (Paper 1). However pectoral muscle hypertrophy accounts for at most 35% of the total increase in lean dry weight between winter and spring. In September, the slightly lower pectoral muscle indices of both adults and first-years compared with winter indices are consistent with some protein having been used on southwards autumn migration (Paper 1). In Dunlins these differences in muscle index between September and winter accounted for only 6% of the total lean dry weight increase. The overall increase in pectoral muscle size in Dunlin between September and May (23.5% in first-years 26% in adults) is very similar to the 25% increase found in first-year Bar-tailed Godwits by Evans & Smith (1975).

The remainder of the spring increase in the lean dry weight of Dunlins is probably due to several factors. Amongst these, hypertrophy of other parts of the musculature, particularly the leg muscles which form part of the protein reserve in geese (Hanson 1962, Ankney 1977), may account for some increase, but since the pectoral muscles amount to about half the total weight of the skeletal muscle in passerines (Ward 1969b) and geese (Ankney 1977), the contribution of any weight increase in these other muscles may be small. Gonad hypertrophy,

particularly in females, may also account for some increase in lean dry weight (Elliot et al. 1976). The lean dry weight increases between September and winter may be partly due to continuing growth in first-years, but this cannot account for the increases in adults. The low weights in September are unlikely to have been induced by moulting since Evans & Smith (1975) found no evidence of moult-induced changes in the protein condition of Bar-tailed Godwits; and in Dunlin the pectoral muscles were not significantly smaller than during winter, as would be expected if the muscle protein reserve was used as a protein source during moult (Paper 1). In the Bullfinch (Newton 1968), the protein reserve was used only to maintain feather growth overnight. A further possibility is that the gastro-intestinal tract becomes longer and heavier in autumn and early winter as a result of a change in diet between summer and winter. Changes of this nature have been found in grouse (Pendergast & Boag 1973) and woodpigeons (Kenwood & Sibley 1978), but this phenomenon has not been investigated in shorebirds.

The adaptive significance of variations in lean weight

In winter, lean weight levels and protein reserves appear to be correlated with the degree of feeding difficulty that may be encountered on each wintering site by shorebirds. In north-east Britain, high winds and low temperatures can simultaneously increase energy requirements and severely curtail feeding, necessitating the use of both fat and protein reserves (Evans & Smith 1975, Dugan et al. 1981, Paper 2). Although lean weights are maintained at a higher level in north-east Britain than elsewhere during the winter, there is no evidence that adults increase their protein reserves in

early winter in advance of severe weather, other than by the replacement of any protein used during autumn migration (Evans & Smith 1975, and Table 2b). First-year shorebirds have smaller protein reserves than adults in autumn and early winter (Paper 1). These reserves are increased such that by January and February, when severe weather is most likely to occur, reserves are similar to those of adults (Evans and Smith 1975, Paper 1). In exceptionally severe or prolonged cold weather the fat and protein reserves carried by shorebirds may be insufficient and some may starve to death (Ash 1964, Marcstrom & Mascher 1979, Baillie 1980, Paper 2).

Because shorebirds do not face severe weather when wintering in equatorial and southern temperate regions (the Austral Summer), they do not require such large protein reserves as in the northern temperate. As these birds increase their lean weights in spring (Table 1), it is unlikely that their winter lean weights are the highest they could attain. Shorebirds wintering in southern and equatorial areas maintain lower lean weights than in north-east Britain. Lean weights are probably similar on most wintering grounds where severe weather is not encountered since Red-necked Stints, Calidris ruficollis, in Tasmania (Thomas & Dartnall 1970) and Pacific Golden Plovers, Pluvialis dominica fulva on Wake Island in the Pacific Ocean (Johnston & McFarlane 1967) have very similar lean weight levels to those in southern Africa. Less reliance should be placed on the lean weight levels indicated for Venezuela (Figure 2), partly because additional corrections had to be made to the published lean weights, and partly because the lean weights probably refer to combined adult and first-year values, although this is not clear from McNeil's (1970) paper.

The latitudinal differences in winter lean weights parallel the differences in the fat reserves of wintering shorebirds. In southern Africa (Summers & Waltner 1979) fat reserves average between only 5% and 7% of body weight in several species including Grey Plovers. Similar average winter fat reserves are carried elsewhere in the absence of severe weather: 9% in Red-necked Stints in Tasmania (Thomas & Dartnall 1970), 5% in plovers and 8% in sandpipers in north-east Venezuela (McNeil 1970), and 11.5% in the Pacific Golden Plover on Wake Island (Johnston & McFarlane 1967). These compare with fat reserves of more than 20% in plovers and 12 - 15% in sandpipers during during mid-winter in north-east Britain (Paper 1). The mid-winter peak in fat reserves that occurs in shorebirds wintering in north-east Britain is absent in birds on equatorial and southern hemisphere wintering grounds.

Some fat may be needed by shorebirds wintering in equatorial and southern hemisphere regions as insurance against reductions in food intake during high temperatures, through reductions in availability of invertebrate prey which may move deeper in the substrate at high temperatures to avoid desiccation (Evans 1976, Dann, in litt.). However shorebirds in mild wintering areas do not need to store reserves for the additional problem of energy balance caused by high windchills that are experienced on northern temperate wintering grounds (Paper 1).

Shorebirds summering (June - July) on equatorial wintering grounds have similar lean weights to the winter level in the same areas. Absence of feeding difficulty is again emphasised by the lipid levels of these summering birds. In Venezuela

(McNeil 1970) these are similar to the lipid levels during the winter and average 9% of total body weight in plovers and 8% in other shorebirds. On Enewetak Atoll (Johnson & Morton 1976) five species of shorebirds had lipid levels between 3% and 7% of total body weight.

There is no evidence of a large premigratory increase in lean weight before departure from the breeding grounds in autumn in either passerines (Baggott 1975) or shorebirds (Johnston 1964) in preparation for any migratory loss; nor are large lipid reserves always recorded in shorebirds during this period (Jehl 1979) although on some migration stopovers extensive fat storage does occur (Paper 1). Shorebirds migrating to southern wintering grounds, particularly those that undertake long-distance non-stop flights (e.g. Knot), may arrive at migration stop-overs in an exhausted condition with very low lean weights (Dick and Pienkowski 1979). These birds must replenish severely depleted lean weights, whether for further migration or to achieve wintering levels, but these levels will be lower than those maintained in northern temperate wintering areas.

In spring, lean weight and protein reserves increase above their winter levels. Some protein may be used during northwards migration, and some is required on the breeding grounds for egg production, and for survival through difficult feeding conditions, particularly snow cover and severe weather, soon after arrival on arctic and subarctic breeding grounds. It is not clear whether all these reserves are carried to the breeding grounds. As during severe weather in mid-winter, the lipid and protein reserves that are carried to the breeding grounds can be insufficient for survival. Morrison (1975)

recorded dead Turnstones, Arenaria interpres, in an emaciated condition on Ellesmere Island in June, and Marcstrom & Mascher (1979) recorded Lapwings and Oystercatchers that had died of starvation during freezing weather soon after their arrrival on breeding grounds in Sweden in late April.

The maximum increases in lean weight between winter and spring on both northern and southern wintering grounds are about 13% (Table 1). Shorebirds do not accumulate all the additional lean weight needed for migration and breeding before spring departure from southern wintering grounds. They must recoup migratory losses and store further protein during migration stopovers. A lean weight increase of 13% in conjunction with the premigratory lipid levels of up to 45% of body weight carried in spring (Johnston & McFarlane 1967, Summers & Waltner 1979, Paper 1), results in total body weight being at least doubled. This may be the maximum weight increase that can be carried (Pennycuick 1969, 1978).

Since females have an additional protein requirement for egg production in spring, they might be expected to carry larger protein reserves to the breeding grounds than males. However, there is no evidence of a sexual difference in the size of the pectoral muscles in Dunlin (Table 2b) before departure for the breeding grounds, and there is insufficient information available for the point to be examined in other species.

The seasonal and latitudinal changes in the lean weights of shorebirds are summarised in Figure 7.

First-years follow a similar pattern of lean weight changes as adults, but their lean weights in winter, and particularly in autumn, are lower than those of conspecific adults (Table 2a; Paper 1). At these times of year first-years

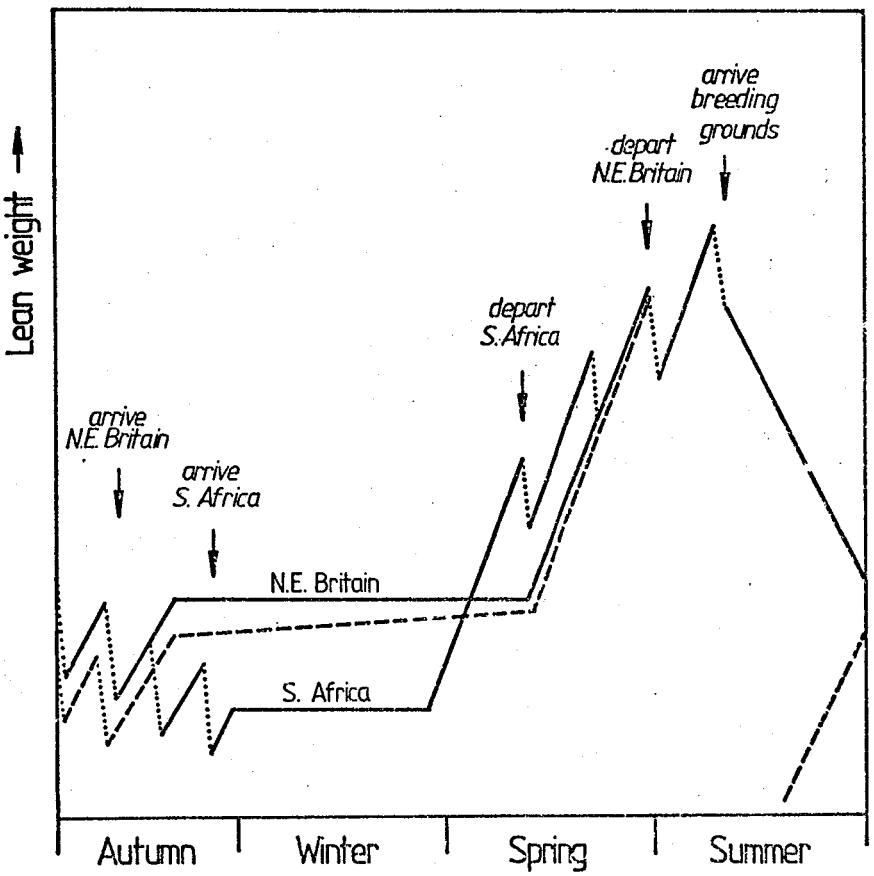

Figure 7. Summary of the seasonal and geographical changes in the lean weight of arctic-breeding shorebirds. For clarity, the seasonal cycles of lean weight are shown for shorebirds wintering in north-east Britain and southern Africa only. ——— are adults, ----- are first-years (shown for north-east Britain only), and ..... indicates periods of migratory flight.

are only a few months old and have not completed growth of musculature (Table 2b, Paper 1). The wings, bills and tarsi of first-year shorebirds are also shorter than those of adults (e.g. Pienkowski & Minton 1973, Dick 1975, Prater, Marchant & Vuorinen 1977). First-year shorebirds complete the growth of their primary feathers at fledging, when they are about one month old, and before they start autumn migration. Apparent age differences in the wing-length/lean weight relationships during autumn and winter (Figures 1 & 3) are mainly a consequence of the short wings of first-year birds.

In north-east Britain the pectoral muscles of plovers (Charadriidae) form a greater proportion of total lean weight than those of sandpipers (Scolopacidae) (Paper 1). Plovers carry this large protein reserve mainly because they experience greater reductions in food intake during severe weather than do sandpipers (Pienkowski 1980) and so must catabolise nutritional reserves more extensively (Paper 2). Despite having larger pectoral muscles, plovers conform to the same regressions of lean weight in relation to wing-length as sandpipers in each season and area. Consequently, other components of total lean weight must form a smaller percentage of lean weight in plovers than in sandpipers. Since water forms a similar percentage of lean weight in both families (Appendix 3) the difference must arise in the lean dry weight of either the skeleton, musculature or internal organs but those concerned cannot be identified.

Waders other than coastal species do not have the same lean weight levels in relation to body size as those reported here. Common Snipe, Gallinago gallinago, in winter have 27%

higher lean weights than predicted from the regression formula (unpublished data). The difference between observed and predicted lean weight is statistically significant ($t_3 = 9.09$ $P < .05$). This higher lean weight level is consistent with species that winter in inland areas encountering harsher weather conditions than coastal species. However Lapwings, Vanellus vanellus (Marcstrom and Mascher 1979) have 30% lower lean weights than predicted, but this may be due to differences in wing-length and wing shape rather than lean weight levels.

SUMMARY

All coastal shorebirds follow the same predictable pattern of seasonal lean weight changes in relation to body size. In adults, lean weights are highest in spring, before departure for the breeding grounds, and lowest after migration in autumn. Adult lean weights in winter are 10% higher in northern temperate areas than in equatorial and southern hemisphere areas. Lean weights in spring increase by up to 13% over their winter level at each wintering area. First-year shorebirds follow a similar pattern to adults but their lean weights in autumn and winter are lower than those of adults. Most changes in lean weight can be attributed to changes in the weight of muscle protein.

The prediction that protein reserves, as measured by lean weight, change seasonally and geographically in the same way as fat reserves is confirmed.

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Appendix 1: Loss of Weight and Nutritional Condition by Dunlins Calidris alpina and Knots C. canutus during short-term captivity.

INTRODUCTION

Short-term loss of weight in birds occurs under a variety of natural conditions. It has been recorded during overnight roosting in passerines (Newton 1968, Evans 1969a, Ward 1969), during migratory flights (Johnston 1968, Child 1969, Evans 1969b, Dick and Pienkowski 1979) and when severe weather conditions prevent feeding (Paper 2). Additionally, weight losses of birds held temporarily in captivity (without food) have also been recorded in shorebirds (O.A.G. Munster 1975, 1976, Lloyd, Pienkowski and Minton 1979) and other species (e.g. O'Connor 1976, Grammeltvedt 1978, Jones 1980, Shapiro and Weathers 1981). In most cases, losses of both fat and lean components of body weight (including water) are implicated.

During studies of the nutritional condition (Paper 1) and heavy metal loads (Evans and Ward in prep.) of shorebirds in north-east England, some samples of Dunlin Calidris a. alpina and Knot C. canutus caught at Teesmouth (54°35'N 1°35'W) under licence from the N.C.C. were held without food for up to 24 hours before they could be brought back to Durham to be killed so that tissues could be frozen immediately in liquid nitrogen in preparation for heavy metal analyses at later dates. The nutritional conditions of these samples were also examined and, so that the data could be included in the larger analyses (Paper 1), it was necessary to correct their nutritional conditions at death

to those at capture by the addition of the weights of the various body components lost during the period of captivity. In addition to the specific purpose of correcting the weight losses of samples kept in captivity during this study, the rates of weight loss recorded below should be widely applicable to allow correction of the weights of Dunlin and Knot kept in captivity for short periods during ringing and netting operations.

CALCULATION OF LOSSES IN WEIGHT AND CONDITION

The total weight loss of Dunlins in relation to time without food was examined using several sources of information. In the samples collected for heavy metal studies, weight loss was calculated either from the live weights at the time of capture and just before death, or from the weights at death of the captive sample and of a sample killed when first captured on the same day. Additionally, a sample of 10 Dunlins - three males and seven females, sexed by bill-length (Evans and Davidson unpublished data) - were kept in captivity in October 1978 for 21 hours, under the same conditions as the samples collected for heavy metal studies, and weighed at frequent intervals. Birds were weighed with a Pesola spring balance accurate to 0.5 g . All samples were kept in darkened cages without food or water during the period of captivity, either indoors at about 20°C or inside a vehicle.

Weight losses of samples of 20 alpina race Dunlins kept outdoors for 14 hours at the Wash, E. England (Lloyd, Pienkowski and Minton 1979) and of juveniles from Munster, West Germany (OAG Münster 1976) were compared with the

Tees data. So that the weight losses during captivity, expressed as percentages in the Münster samples, were comparable with other data, absolute losses were calculated by multiplying by an average body weight of 55.6 g. (OAG Münster 1976).

Total weight losses in Knots at Teesmouth were calculated as for Dunlins, except that no samples were weighed regularly during their period of captivity.

The weight of fat, water content, pectoral muscle size - used as an index of protein reserve (Kendall, Ward and Bacchus 1973, Evans and Smith 1975, Papers 1 and 2) - and total lean dry weight in captive samples were analysed in relation to time without food. The methods of carcass analysis are described in detail in Paper 1. Because of the methods of heavy metal analysis used (Evans and Ward in prep.), changes in liver weights could not be examined separately.

All the samples analysed for the decline in nutritional condition during captivity were collected during the 1977/78 winter. The duration of captivity varied from four hours to 24 hours on different collection dates (Table 1). Samples collected in mid-September 1977 and late May 1977 and 1978 were excluded from the analysis since nutritional condition can be different at those times of year compared with winter (Paper 1). However, there was no evidence that the rates of loss of condition in these samples differed from those collected during winter. All samples were caught in cannon-nets at the same stage of the tidal cycle (between two hours before high water, and high water), so any differences in the rates of decline in nutritional condition due to capture

Table 1. Dates of collection, duration in captivity and sample sizes of Dunlin and Knot from Teesmouth during the 1977/78 winter.

Date	Time in Captivity (hours)	No. of Dunlin			No. of Knot		
		Total	Male	Female	Total	Male	Female
12.10.77	20	13	1	12			
10.11.77	20	10	4	6	10	4	6
9.12.77	0	5	4	1	2	1	1
	4	14	7	7	8	4	4
26.01.78	0				1		1
9.02.78	0	14	5	9	4	2	2
	24	12	7	5	11	5	6
15.02.78	8	10	3	7			
7.03.78	18				7		7

at different stages of the tidal feeding cycle should be minimized.

LOSSES IN WEIGHT AND CONDITION DURING CAPTIVITY

1. Total Body Weight

Decrease in the total body weight of Dunlins occurred in two distinct phases: up to and after the first eight hours of captivity. During the first phase, weight loss by Dunlins at Teesmouth and on the Wash followed a very similar pattern (Figure 1), with the highest rate of loss during the first hour of captivity and somewhat lower rates thereafter. In Teesmouth samples, weight losses were closely similar in the regularly-weighed sample (from October 1978) and in the samples from the winter of 1977/78 that were weighed only at the start and end of captivity. Absolute rates of weight loss were higher in females than males, with total losses after 8 hours of 4.3 g. and 3.5 g. respectively. The extent of weight losses during the first eight hours of captivity of individuals in the October 1978 sample was strongly correlated with weight at capture (r_8 = .885 $P < .001$). The rate of weight loss in the sample of unsexed Dunlins from the Wash was similar to the rate for female Dunlins at Teesmouth, either because most of the Wash sample were females or because these birds were kept outdoors and may therefore have been subjected to lower temperatures than the Teesmouth samples. Dunlins from Munster lost weight at a similarly low rate to males at Teesmouth, probably because the former were first-years in autumn, when their weights are very low (Paper 3).

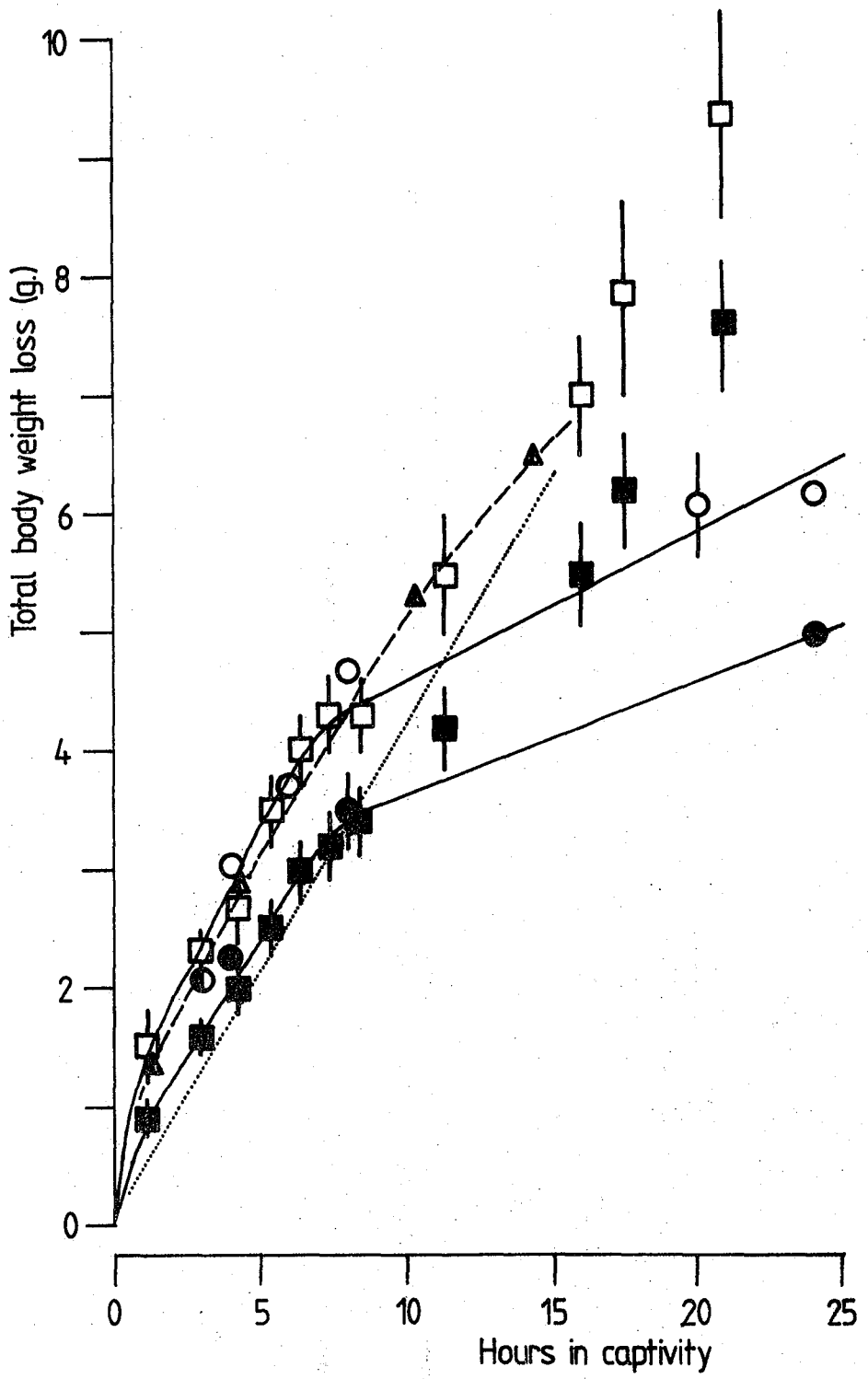

Figure 1: Loss of total body weight by Dunlins starved in captivity. Open symbols are females, solid symbols are males and halved symbols are unsexed. Squares are 7 males, 3 females from Teesmouth weighed over 21 hours in October 1978, circles and solid lines are other samples from Teesmouth during 1977/78 kept undisturbed after capture. Triangles and dashed line show a sample from the Wash, from Lloyd, Pienkowski and Minton (1979). The dotted line shows estimated losses in northern Germany, derived from OAG Munster (1976). Points show the mean ± 1 standard error, where available.

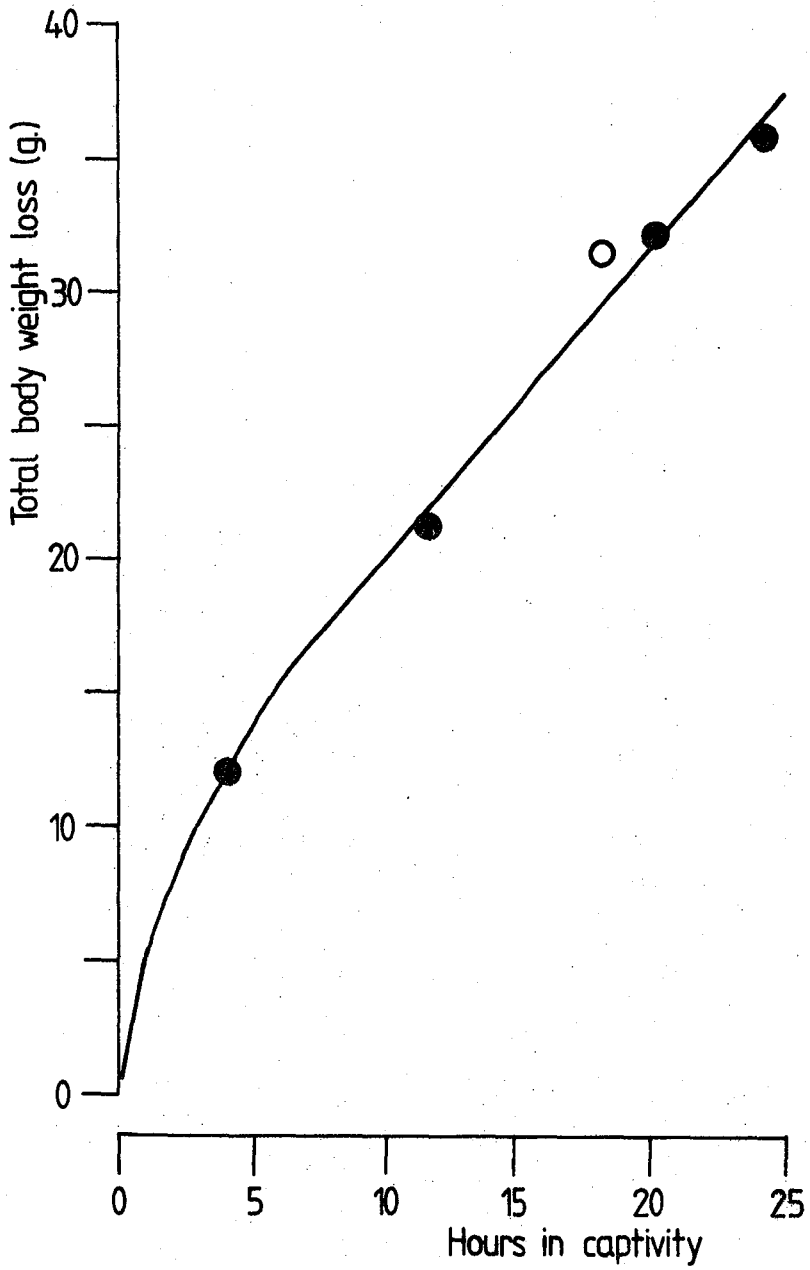

Figure 2: Loss of total body weight by Knots from Teesmouth starved in captivity. Samples were undisturbed during their period of captivity. ○ indicates a sample of females. ● indicates combined sexes. Trend line fitted by eye.

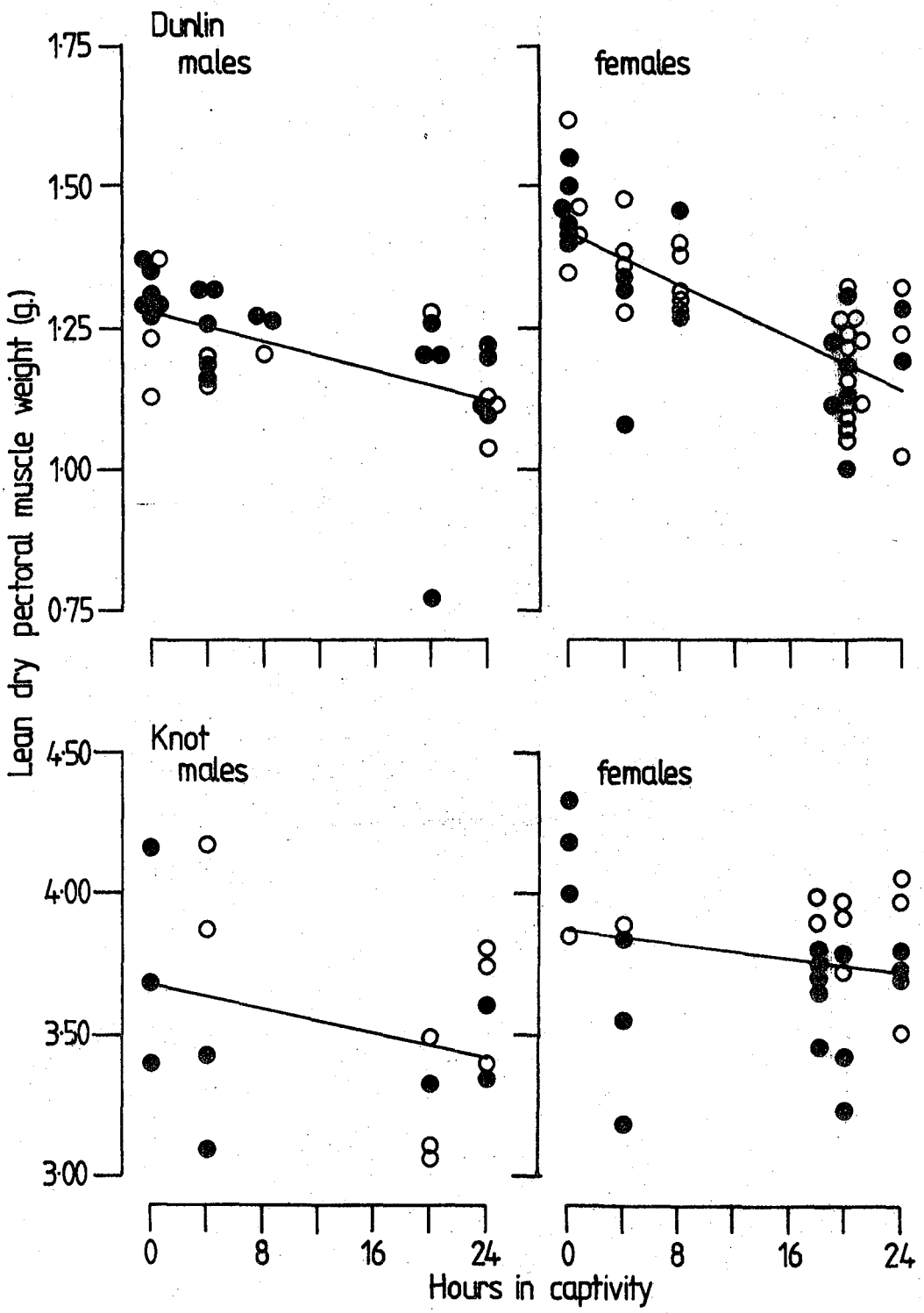

Figure 3: Loss of lean dry pectoral muscle weight by adult (●) and first-year (○) Dunlins and Knots from Teesmouth starved in captivity. Solid lines show least-squares regressions: Dunlin males $r_{29} = -.56$, $b = -.007$, $P < .001$, females $r_{45} = -.75$, $b = -.012$, $P < .001$; Knot males $r_{14} = -.33$, $b = -.011$, $P > .10$, females $r_{25} = -.22$, $b = -.006$, $P > .10$.

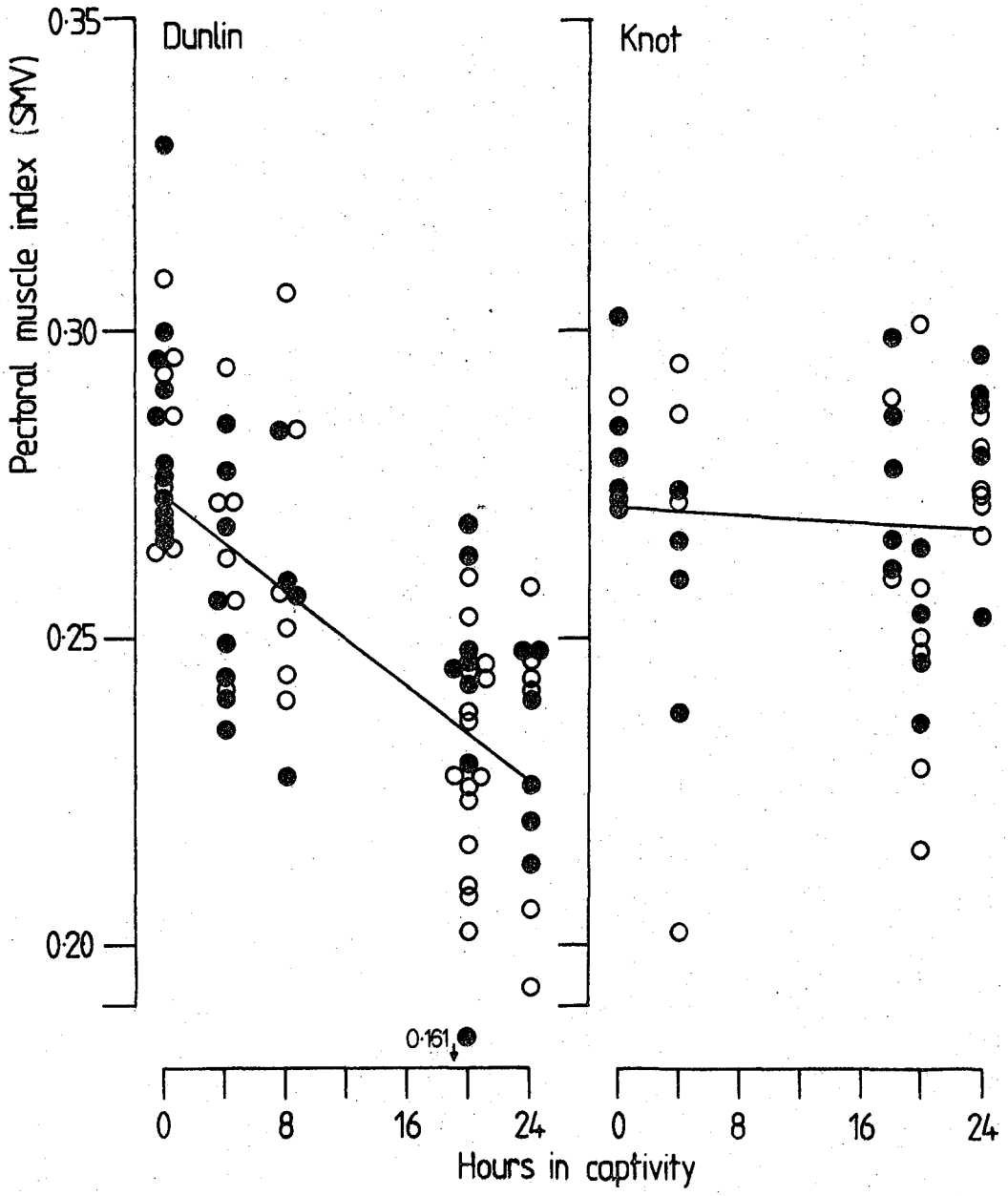

Figure 4: Pectoral muscle indices (SMV) of adult (●) and first-year (○) Dunlins and Knots from Teesmouth starved in captivity. Solid lines show least-squares regressions: Dunlin $r_{76} = -.62$ $b = -.002$ $P < .001$, Knot $r_{41} = -.05$, $b = -.0001$ $P < .10$.

Rates of weight loss after eight hours of captivity depended on the treatment of the captive birds. Repeatedly weighed Dunlins from Teesmouth and the Wash continued to lose weight rapidly but at a slower rate than in the first 8 hours (Figure 1). Females continued to lose more weight more rapidly than males. In the October 1978 sample, the weight lost during the second phase (8 - 21 hours after capture) was again strongly correlated with weight at capture (r_8 = .749 $P < .02$). Much less weight was lost during the second phase by Dunlins that were undisturbed until the end of their captivity than by the birds weighed repeatedly. In undisturbed samples after 24 hours of starvation in captivity, females had lost an average of 6.2 g. and males 5.0 g. , corresponding to losses of 11.2% and 10% of body weight. This compares with weight losses of 18.5% and 16.6% in repeatedly weighed males and females after 21 hours of captivity.

Loss of total body weight by Knots followed the same two-phase pattern as Dunlins (Figure 2), with a loss of 18 gms. during the first eight hours of captivity and a steady loss of 1.15 g. hr^{-1} thereafter. After 24 hours the loss averaged 36 g. , corresponding to 22.8% of total body weight, i.e. about twice the equivalent weight loss in Dunlins. A sample of females lost 31.5 g. in 18 hours, about 2 g. more than expected from mixed-sex samples.

2. Pectoral Muscles

In Dunlins, a steady, significant, decline in lean dry pectoral muscle weight started within four hours of capture. The rate of loss was greater in females than males (Figure 3).

Over 24 hours of captivity males lost 0.16 g. (12.4% of the lean dry pectoral muscle) and females lost 0.29 g. (20.4%). (The total weights of lean dry pectoral muscle material lost during captivity are in fact twice the values given above since these refer to one pectoral muscle block only. Percentage losses remain the same.)

In Knots, lean dry pectoral muscle weight decreased only slightly, and not significantly (Figure 3), with losses averaging 0.26 g. in males and 0.14 g. in females (7.1% and 3.6% of lean dry pectoral muscle weight respectively).

Expressing lean dry pectoral muscle weight as a proportion of a standard muscle volume (SMV) removes variation due to body size. (For details of the derivation of this index see Paper 1.) Pectoral muscle indices of Dunlins decreased significantly (r_{76}= -.616 $P < .001$) during captivity (Figure 4) with a loss of 16.7% in 24 hours. In contrast, the pectoral muscle indices of Knots declined by only 0.9% over 24 hours. The absence of a decline in pectoral muscle size in Knots is not caused by seasonal variations in muscle size since the pectoral muscle indices of samples killed on capture and held in captivity on 9 February 1978 did not differ.

3. Lean Dry Body Weight

Total lean dry body weight also decreased gradually from the start of captivity (Figure 5). In Dunlins, this decrease was significant in females (r_{45}= -.455 $P < .01$) but not in males (r_{29}= -.212 $P > .10$). Over 24 hours losses amounted to 1.50 g. (8.6% of lean dry weight) in females, but only 0.58 g. (3.6%) in males. These values include the losses of pectoral muscle material described above:

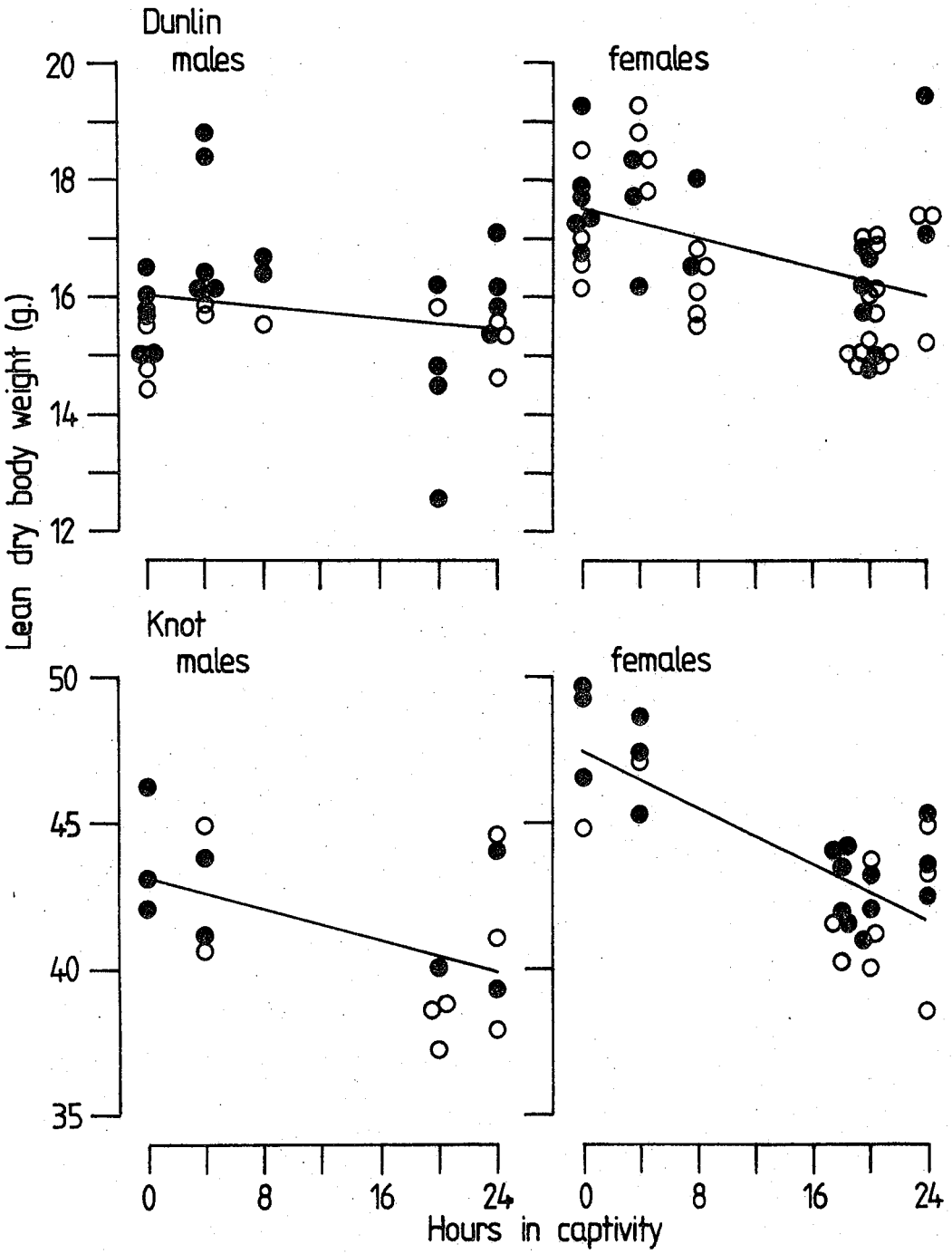

Figure 5: Total lean dry body weights of adult (●) and first-year (○) Dunlins and Knots from Teesmouth starved in captivity. Solid lines show least-squares regressions: Dunlin males $r_{29} = -.21$, $b = -.024$ $P > .10$, females $r_{45} = -.46$, $b = -.062$ $P < .01$; Knot males $r_{14} = -.50$, $b = -.13$ $P < .05$, females $r_{25} = -.76$, $b = -.246$ $P < .001$.

losses of other components of lean dry weight averaged 0.92 g. in females and 0.26 g. in males over 24 hours.

Lean dry body weights of Knots also decreased during captivity (Figure 5), significantly in both males (r_{14}= -.500 P < .05) and females (r_{25}= -.759 P < .001). Females lost more weight than males, in 24 hours averaging 5.89 g. and 3.23 g respectively. Corresponding percentage losses were 12.4% and 7.5% of lean dry body weight. Losses of other components than pectoral muscles were 5.61 g in females and 2.71 g in males over 24 hours.

4. Water Content

Water content (water as a percentage of total lean weight) did not follow the steady decreases in dry body components. Dehydration occurred in both Dunlins and Knots and was most rapid during the first four hours of captivity (Figure 6). In this period water content as a percentage of total lean weight decreased from 65.8% to 61.8% in Dunlins (t_{32} = 39.13 P < .001) and from 66.7% to 63.5% in Knots (t_{13} = 10.04 P < .001). Thereafter water content (expressed as a percentage) did not change in Dunlins, but a reduced rate of dehydration continued in Knots: after 24 hours water content averaged only 60.9%.

5. Fat

The large individual and seasonal variations in the weight of fat carried by shorebirds (Paper 1) makes assessment of the rates of utilization of fat reserves during captivity impossible by the methods used above to estimate changes in lean body components, particularly because the duration of captivity varied between samples from different months.

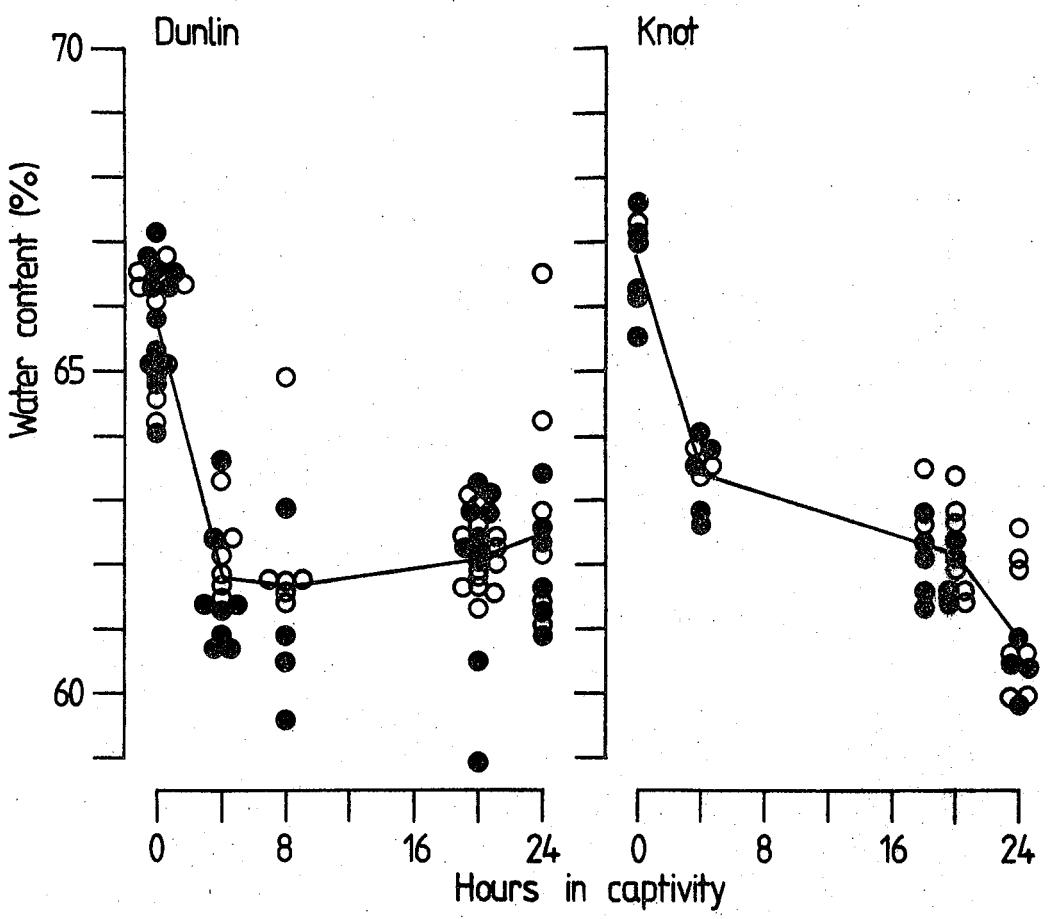

Figure 6: Water contents (water as a % of total lean weight) of adult (●) and first-year (○) Dunlins and Knots from Teesmouth starved in captivity. Solid lines join mean values.

Furthermore, since dehydration and the loss of lean dry material also cause changes in the total body weight during captivity, the lipid index (fat as a percentage of total body weight) cannot be used to calculate rates of fat catabolism. In Knots, sample sizes are too small to permit comparison between samples killed at capture and kept in captivity on the same day. Fat loss in Knots was therefore calculated as the difference between total weight loss and lean weight loss. This yields a rate of 0.308 g. fat hr^{-1}, and indicates that fat catabolism started after eight hours in captivity.

Sufficiently large samples of Dunlins from 9 February 1978 were collected for rates of fat loss to be calculated for that day (Table 2). Assuming that, as for Knots, fat reserves began to be mobilised more rapidly eight hours after capture, the rates of loss of fat were 0.132 g. hr^{-1} in males and 0.152 g. hr^{-1} in females. When differences in body size and metabolic rate are taken into account (Table 3), the rates of fat catabolism were very similar to those in Knots, i.e. between 0.7 - 0.8% of lean body weight per hour.

DISCUSSION

Much of the initial loss of weight by Dunlins and Knots starved in captivity was due to water loss. The initial decline in water content was at least partly caused by water loss associated with defecation (Lloyd, Pienkowski and Minton 1979), but evaporative water loss was probably also involved. The most rapid dehydration occurred during the first four hours of captivity. Thereafter water was lost by

Dunlins in proportion to the loss of lean dry weight (i.e. the percentage water content stabilised). Dehydration in Knots continued at a much reduced rate. Under natural conditions of starvation when severe weather prevents feeding, no significant change in the percentage water content of shorebirds occurs (Marcstrom and Mascher 1979, Paper 2), but dehydration has been recorded in various species deprived of water during long migratory flights (Searle 1956, Moreau and Dolp 1970, Fogden 1972). Evaporative water loss increases with temperature (Tucker 1968), and in the Dunlins and Knots might have been accelerated by any rise in body temperature caused by capture stress (Henschel and Louw 1978). After the initial few hours of captivity, further dehydration may be minimised by the production of water during fat and protein metabolism, and by a gradual decrease in body temperature back to its normal level (Henschel and Louw 1978), in conjunction with lower lean dry weights. Body temperature in fasted American Kestrels Falco sparverius declined continuously below normal for three days (Shapiro and Weathers 1981). Production of metabolic water alone is usually insufficient to balance water loss (Tucker 1968).

Capture stress probably had a major effect on the rates at which components of dry body weight were lost during captivity in the present study. In passerines (Nisbet and Medway 1972, Leberman and Stern 1977), Dunlins (Fuchs 1973) and Semipalmated Sandpipers (Page and Middleton 1972) held only briefly in captivity capture stress is known to induce weight losses that last for at least seven days. In pigeons and doves, Henschel and Louw (1978) recorded a rapid shift to

Table 2. Loss of fat in Dunlin starved in captivity for 24 hours.

	Fat (g.)[1]		Mean fat loss (g.)	Mean rate of fat loss (g. hr^{-1})[2]
	At capture	Starved		
Males	5.35 ± .47(5)	3.23 ± .52(7)*	2.12	.132
Females	4.88 ± .53(9)	2.45 ± .64(5)*	2.43	.152

[1] Values are mean ± 1 standard error (sample size).

[2] Assuming fat reserve metabolism began 8 hours after capture (see text).

* Weights of fat in starved samples is significantly less (Student's t $P < .05$) than at capture.

Table 3. Comparison of the rates of fat metabolism in Dunlin and Knot in relation to body size.

		Rate of fat loss (g. hr^{-1})	Lean Wt.$^{.75}$ (g.)	Fat metabolism index+
Dunlin	male	.132	18.21	.0073
	female	.152	19.36	.0079
Knot		.308	40.07	.0077

\+ Fat metabolism index = $\frac{\text{rate of fat loss}}{\text{lean weight}^{.75}}$

anaerobic metabolism on capture, with metabolic acidosis lasting for at least six hours, and evidence of functional or structural changes in muscle tissue. These latter may account for the loss of pectoral muscle tissue in Dunlins starting very soon after capture. This loss, averaging 16.4% in 24 hours is similar to the loss of 10% of pectoral muscle weight in 12 hours in House Sparrows Passer domesticus kept overnight (Jones 1980) under similar conditions to the shorebirds in this study. However, it is unlikely that the reason suggested for the loss of pectoral muscle tissue by House Sparrows - the replacement of proteins denatured during temporary starvation - is the main cause in Dunlins because of the rapid onset of muscle loss after capture, when food probably still remained in the gut. Indeed, much of the loss in pectoral muscle weight in House Sparrows (Jones 1980) occurred during the first six hours of captivity and may also be attributable to the effects of capture stress. The absence of any loss of pectoral muscle tissue in Knots kept under the same conditions as the Dunlins is a further indication that the losses, probably protein, from the pectoral muscles are not necessarily due to a high requirement for replacement proteins. It also suggests the existence of interspecific differences in the effects of capture stress, even amongst congeners. However, Knots could have obtained their protein requirements from other parts of the musculature, possibly leg muscles. These were not examined separately in this study, but are known to form a protein store in Geese (Hanson 1962, Ankney 1977).

Sources of lean dry weight losses from other than the pectoral muscles are not known, but must be either other

muscles, or organs such as the liver. Large short-term variations in the liver weight of birds are well-known. Overnight, Redwinged Blackbirds Agelaius phoeniceus lost up to 30% of liver weight (Fisher and Bartlett 1957), and the average liver weight of juvenile Willow Warblers Phylloscopus trochilus was higher in the evening than the morning (Baggott 1977). Grammeltvedt (1978) found liver weight losses of 25% in Willow Grouse Lagopus lagopus and 43% in Bantam Hens Gallus gallus starved for between four and seven days, such that the loss of total body weight was about 20%, and O'Connor (1976) recorded a 62% decrease in the lean dry liver weight of nestling Blue Tits Parus caerulescens starved overnight in captivity. In shorebirds that had starved to death during severe weather, lean dry liver weight decreased by 71% in Lapwings Vanellus vanellus and 60% in Oystercatchers Haematopus ostralegus (Marcstrom and Mascher 1979), and 69% in Redshanks Tringa totanus (my own unpublished data). These liver losses were greater than the losses of lean dry body weight, which averaged 45%, 35% and 27% respectively.

Fat catabolism in Dunlins and Knots did not occur at a significant rate until about eight hours after capture. Before this, sufficient energy for metabolic requirements must have been available from the digestion of food in the gut and from breakdown of glycogen in the liver. The rates of fat reserve metabolism during captivity suggest that Dunlins and Knots were using energy at a minimum of 3.3 - 3.6 x Basal Metabolic Rate (Table 4). These values, similar to the 2.9 x BMR in captive Bar-tailed Godwits (Smith 1975), are high considering that the birds were warm and relatively

Table 4. Metabolic rates of Dunlins and Knots during the period of fat catabolism in captivity.

	Rate of fat loss ($g.\ hr^{-1}$)	Energy value ($Kcal.hr^{-1}$)[1]	Basal metabolic rate ($Kcal.hr^{-1}$)[2]	Metabolic rate (x BMR)
Dunlin male	.132	1.20	0.363	3.31
female	.152	1.38	0.385	3.59
Knot	.308	2.80	0.776	3.61

[1] Assuming calorific value of fat = 9.1 $Kcal.g.^{-1}$.

[2] Calculated from Lasiewski and Dawson (1967).

inactive, and that free-living shorebirds expend energy at 4 - 7 x BMR (Smith 1975, Goss-Custard 1977) and again may result from capture stress. Shapiro and Weathers (1981) found indications in decreasing BMR of fasted American Kestrels of active supression of metabolism. This might partially compensate for capture stress increasing BMR. The severity of the stress imposed during captivity affected the rate at which Dunlins lost weight after the initial eight hours of captivity. Birds that were handled and weighed regularly lost weight more rapidly than birds that were not handled between capture and the end of their period of captivity. The components contributing to this high rate of weight loss in the regularly weighed birds are not known, but were probably a continuing dehydration due to increased locomotor activity and continuing raised body temperature (Henschel and Louw 1978), and a higher rate of reserve fat metabolism. Rates of weight loss during the first eight hours of captivity changed little, regardless of the severity of the imposed stress, probably because the major contributor to weight loss in this period was dehydration associated with defecation. Weight losses from this period should be widely applicable to the correction of weights in Dunlins and Knots held under a variety of conditions, but weight corrections for more than eight hours of captivity can only be made according to the conditions of captivity. Information presented here emphasises the importance of capture stress in causing major disturbances to the nutritional condition of shorebirds.

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Appendix 2: The estimation of Lean Weight and Fat Reserves for Live Shorebirds.

Several authors have provided formulae for the estimation of lean weight and lipids for single species of shorebirds, based on the relationship between wing-length and weight (McNeil & Cadieux 1972, Page & Middleton 1972, Mascher & Marcstrom 1976, Pienkowski, Lloyd & Minton 1979). Most of these formulae are derived from samples collected during autumn migration in the northern temperate region. Because of seasonal and latitudinal lean weight variation (Paper 3), these cannot be used to estimate lean weights in other areas and during other seasons. The only published formula for the calculation of winter lean weights is for Dunlin, Calidris a. alpina (Pienkowski, Lloyd & Minton 1979).

Sufficient samples of shorebirds have been collected in north-east Britain during winter (November - March) to allow formulae for the estimation of lean weight from wing-length and bill-length to be derived for several species. The best estimates of lean weight are given by multiple regressions on wing-length and bill-length (Table 1). Where one measurement is missing, either wing-length or bill-length can be used to estimate lean weight in most species (Table 2), but with reduced accuracy of estimate. It should be noted that the single measurement giving the more accurate estimate differs between species and age classes. Most shorebirds are sexually dimorphic in size, with females larger than males (see Prater, Marchant & Vuorinen 1977, Paper 1), but there were no improvements in the correlations when males and females were

examined separately. Both sexes have therefore been included in the same formulae. Where possible, separate regressions are given for adults and first-years since first-years have not completed growth in winter and have lower lean weights than adults of the same size. The weight of fat is calculated by subtraction of the estimated lean weight from the total body weight.

Some published formulae for estimating lean weights and lipids have been based on inhomogeneous samples collected in different seasons, and involving different age classes. Care should be exercised if these formulae are used, because of seasonal and age differences in lean weight. No formulae should be used for seasons other than those from which they were derived.

For species other than those listed in Tables 1 and 2, and for other seasons and areas, lean weight estimates for any coastal shorebird species can be obtained from some of the overall regression formulae for shorebirds (Paper 3) since all species adopt similar lean weight levels with respect to body size, and follow the same pattern of lean weight change. These formulae are listed in Table 3. As the formulae are derived from the mean values for each species, and as the slopes of the single-species regressions (Table 2) differ from those of the overall regressions, estimates of lean weight should be made from the mean wing-length of a live sample. Since some of the error in fitting the regression lines is caused by the errors in estimating wing-lengths appropriate to published lean weights, the error of a lean weight estimate, calculated from all formulae other than those for north-east Britain during winter, may be artificially large.

For adults, the formula for winter in north-east Britain is probably valid for shorebirds wintering in most northern temperate areas, where feeding difficulty caused by severe weather may be encountered during the winter. Similarly, the formula derived from shorebirds wintering in southern Africa is probably valid for many southern hemisphere and equatorial wintering areas. As discussed in Paper 3, lean weight formulae for Venezuela, calculated from McNeil (1970), should not be used for lean weight estimation, because they are derived from combined adult and first-year samples, and because of possible inaccuracies resulting from the corrections for missing body components made to the published lean weights.

The estimation of lean weights during migration periods, particularly in spring, is difficult because lean weights change rapidly. Insufficient information is currently available to quantify these changes because lean weights vary greatly depending on the length of stay at a migration stopover. An approximate estimate of the spring lean weight of a shorebird shortly before its departure from a migration stopover can be made by the addition of 13% to the winter lean weight in that area. Lean weights do not change so markedly during autumn migration, and the formula for adults in the northern temperate region may be used. Autumn lean weights at more southerly sites are probably close to the winter levels in these areas, so the winter formula for southern Africa can be used to indicate lean weights.

The continuing growth of first-years during autumn and winter means that estimates of their lean weight may be less accurate than those of adults because lean weights are based on averages from several months.

None of the formulae listed in Tables 1 - 3 that use wing-length as an estimator of body size can be used to estimate the lean weight of birds undergoing moult of the outer primary feathers. For moulting birds, estimates for north-east Britain during winter can be made from bill-length formulae. All formulae for lean weight estimation should be used only for shorebirds that are in 'normal' condition for the time of year. Where there is evidence that birds are in poor condition, for example with very low fresh weights during severe weather or after arrival from a migratory flight in an exhausted state, the formulae cannot be used. Estimation of the size of the pectoral muscles (Davidson 1979) can be used as a guide to the applicability of lean weight estimation formulae to a sample of live birds.

Table 1. Formulae for the estimation of lean weight (LW), in grams, of shorebirds in north-east Britain during winter (November - March) from wing-length (WL) and bill-length (BL), in millimetres.

Species	Age	n	Formula	r	r^2	1 s.e. of $LW^{1/3}$
Calidris a. alpina	Ad.	40	$LW = (.0053WL + .0151BL + 2.580)^3$	.674****	.454	.0635
	1st-yr.	32	$LW = (.0105WL + .0116BL + 2.024)^3$	.692****	.479	.0566
Pluvialis apricaria	Ad.	16	$LW = (.0179WL + .0386BL + 1.367)^3$	.712**	.507	.1183
Limosa lapponica	Ad.	19	$LW = (.0012WL + .0183BL + 4.747)^3$	.837****	.700	.1747
	1st-yr.	13	$LW = (.0090WL + .0166BL + 3.113)^3$	.853**	.728	.1400
Tringa totanus	Ad.	12	$LW = (.0138WL + .0223BL + 1.962)^3$	.897***	.805	.0539
	1st-yr.	8	$LW = (.0149WL - .0518BL + 4.770)^3$	.852*	.725	.0510

Significance levels are: **** $P < .0001$, *** $P < .001$, ** $P < .01$, * $P < .05$.

Table 2. Formulae for the estimation of lean weight (LW), in grams, of various shorebirds in north-east Britain during winter (November - March) from either a) wing-length, in millimetres, or b) bill-length, in millimetres

Species	Age	n	Formula	r	r^2	1 s.e. of $LW^{1/3}$	P
a) Wing-length:							
Calidris a. alpina	Ad.	40	$LW = (.0142WL + 1.987)^3$	.564	.318	.0700	<.001
	1st-yr.	32	$*LW = (.0166WL + 1.670)^3$	.627	.393	.0600	<.0001
Pluvialis apricaria	Ad.	16	$*LW = (.0232WL + 1.239)^3$	.693	.480	.1212	<.01
Limosa lapponica	Ad.	19	$LW = (.0194WL + 2.321)^3$	.708	.502	.2171	<.001
	1st-yr.	13	$LW = (.0235WL + 1.390)^3$	.736	.542	.1716	<.02
Tringa totanus	Ad.	12	$*LW = (.0192WL + 1.975)^3$	.851	.724	.0608	<.0005
	1st-yr.	8	$*LW = (.0101WL + 3.426)^3$	.533	.284	.0752	>.10
b) Bill-length:							
C. a. alpina	Ad.	40	$*LW = (.0193BL + 3.075)^3$	.657	.432	.0639	<.0001
	1st-yr.	32	$LW = (.0192BL + 3.052)^3$	.617	.381	.0606	<.001
C. canutus	Ad.	29	$*LW = (.0258BL + 4.343)^3$	.463	.214	.1024	<.02
	1st-yr.	19	$*LW = (.0207BL + 4.493)^3$	.519	.270	.0733	<.05
P. apricaria	Ad.	16	$LW = (.0743BL + 3.968)^3$	.528	.279	.1427	<.05
L. lapponica	Ad.	19	$*LW = (.0192BL + 4.946)^3$	.836	.699	.1687	<.0001
	1st-yr.	13	$*LW = (.0220BL + 4.597)^3$	.831	.691	.1411	<.0005
T. totanus	Ad.	12	$LW = (.0457BL + 3.307)^3$	.766	.587	.0744	<.01

* indicates the formula that gives the best lean weight estimate for each species and age-class. Wing-lengths were not available for Knot C. canutus.

Table 3. Formulae for the estimation of lean weight (LW), in grams, from wing-length (WL), in millimetres, for shorebirds in various areas and seasons.

Season	Area	Age	n	Formula	r	r^2	1 s.e. of $LW^{1/3}$
Winter	N.E. Britain	Ad.	9	$LW = (.0294WL + .0775)^3$	.9991	.9982	.1066
		1st-yr.	4	$LW = (.0294WL + .1534)^3$	.9995	.9990	.0610
Winter	Southern Africa	Ad.	7	$LW = (.0292WL - .0582)^3$	.9994	.9987	.0375
Autumn	N. Temperate	Ad.	11	$LW = (.0284WL + .0316)^3$	.9919	.9838	.1796
		1st-yr.	7	$LW = (.0296WL - .1323)^3$	.9922	.9844	.1810
Summer	Enewetak Atoll	Ad.	4	$LW = (.0289WL - .0922)^3$	.9920	.9841	.1921

Significance for all formulae $P < .0001$, except first-years in N.E. Britain in winter ($P = .0005$) and Enewetak Atoll in summer ($P < .01$).

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Appendix 3: Water content[a] of shorebirds in north-east Britain

	Adults		First-years	
	n	$\bar{x} \pm 1$ s.d.	n	$\bar{x} \pm 1$ s.d.
a) Autumn:				
Ringed Plover	3	68.43 ± 1.14		
Sanderling			1	68.45
b) Winter:				
Ringed Plover	1	71.57		
Golden Plover[b]	20	64.45 ± 1.91		
Grey Plover	3	68.07 ± 1.24		
Knot	10	66.76 ± 0.75	2	67.79 ± 0.75
Sanderling	8	66.71 ± 1.19	3	66.41 ± 0.92
Dunlin	58	67.54 ± 2.20	35	67.50 ± 1.48
Bar-tailed Godwit	23	66.64 ± 1.77	15	66.58 ± 1.33
Curlew[b]	11	74.94 ± 2.57		
Redshank[c]	12	68.17 ± 1.58	8	68.38 ± 1.01
Turnstone	1	67.45 ± 1.91	4	67.09 ± 1.47
c) Spring				
Ringed Plover	3	67.58 ± 3.88		
Sanderling	7	63.84 ± 4.07		
Dunlin	2	66.86 ± 2.19	1	68.24

a Water Content = $\frac{\text{Water (g.)}}{\text{Lean Wt. (g)}}$ x 100%

b All treated as adults.

c Redshanks were from the Ythan estuary, north-east Scotland; all other species were from Teesmouth and Lindisfarne.